



The role of spatial memory and frames of reference in the precision of angular path integration

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ABSTRACT

Angular path integration refers to the ability to maintain an estimate of self-location after a rotational displacement by integrating internally-generated (idiothetic) self-motion signals over time. Previous work has found that non-sensory inputs, namely spatial memory, can play a powerful role in angular path integration (Arthur et al., 2007, 2009). Here we investigated the conditions under which spatial memory facilitates angular path integration. We hypothesized that the benefit of spatial memory is particularly likely in spatial updating tasks in which one's self-location estimate is referenced to external space. To test this idea, we administered passive, non-visual body rotations (ranging 40°–140°) about the yaw axis and asked participants to use verbal reports or open-loop manual pointing to indicate the magnitude of the rotation. Prior to some trials, previews of the surrounding environment were given. We found that when participants adopted an egocentric frame of reference, the previously-observed benefit of previews on within-subject response precision was not manifested, regardless of whether remembered spatial frameworks were derived from vision or spatial language. We conclude that the powerful effect of spatial memory is dependent on one's frame of reference during self-motion updating.

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1. Introduction

Spatial orientation and navigation are complex cognitive behaviors exhibited by humans as well as other mobile species, including ants, bees, and hamsters to name a few (Etienne, Berlie, Georgakopoulos, & Maurer, 1998). Spatial orientation and navigation require the integration of sensory information arising from multiple modalities, thereby allowing us to keep track of self-motion and update our position relative to a known location in external space. One area of research concerns how self-motion cues are combined to produce a unitary percept of translational and rotational displacements during nonvisual locomotion. Vision provides multiple sources of information for determining self-position and orientation in external space. However, in the absence of vision, we retain the ability to remain oriented by relying upon internally-generated (idiothetic) self-motion signals such as proprioceptive cues from the musculature and acceleration signals from the vestibular apparatus (Berthoz, 1996; Highstein, 1996; Israël & Berthoz, 1989). As one can imagine, the ability to accurately and precisely detect self-motion in space without visual input confers biological advantages. In these situations, the brain must complete the critical

computational process of integrating sensory signals over time. The process of updating based solely on idiothetic information is known as *path integration* (or sometimes “dead reckoning” in the animal literature; see Etienne, Maurer, & Séguinot, 1996; Mittelstaedt & Mittelstaedt, 1980, 2001; Whishaw, Hines, & Wallace, 2001). *Angular path integration* is a special case of path integration, specifically involving updating during angular self-motion (Loomis, Klatzky, Golledge, & Philbeck, 1999; Loomis et al., 1993). Signals representing the angular motion of the head in three-dimensional space (i.e., yaw, pitch, and roll) are transduced by the vestibular end organs in the inner ear. Angular displacement is derived through the temporal integration of velocity signals and the double integration of acceleration signals generated in three semicircular canals on each side of the head; these signals are then transmitted to the central nervous system via vestibular afferents in the eighth cranial nerve (Berthoz, 1996; Highstein, 1996).

Much research has been focused on the relative contribution of redundant sensory inputs (i.e., vestibular, proprioceptive, and efference copy signals) to path integration when vision and audition are unavailable (for a review see Harris et al., 2002; see also Lackner & Dizio, 2005). Here, the typical research paradigm involves isolating the role of an individual sensory system by reducing the set of cues available from other sensory systems (e.g., diminishing the environmental context and/or reducing visual input between trials). Although these “low-level” cues play an important role in determining the magnitude of head and body rotations, “higher-level” (non-

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sensory) inputs are significant factors as well. Previous work in our laboratory has demonstrated that spatial memory dramatically enhances angular path integration, which is manifested as increased *within-subject response precision* in tasks requiring participants to indicate their current position or orientation (Arthur, Philbeck, & Chichka, 2007, 2009). In these studies, we hypothesized that remembering an environment while navigating without vision yields a more precise self-location estimate. This may be subjectively experienced as an increased certainty in one's current estimate of position and orientation. As one moves away from a known location when traveling without vision, noise in the self-motion signals will tend to accumulate over time, yielding an increasingly *imprecise* estimate of one's position and orientation. If one has access to an internal representation of the surrounding environment while moving without vision, however, this provides a structured spatial framework that could potentially facilitate integration of incoming sensory self-motion information into one's updated position or orientation estimate. Response precision is thought to be informative about the precision of the underlying spatial representations updated during body motions (Mergner, Nasios, Maurer & Becker, 2001). In this view, when responding, participants are in effect sampling from a distribution of possible positions or orientations. Any uncertainty in the position/orientation estimate will be reflected in the variance of the distribution of behavioral responses. To test these predictions, in our past work (Arthur et al., 2007, 2009), we administered passive, whole-body stimulus rotations about an earth-vertical axis in darkness and asked participants to manipulate a pointer to indicate the magnitude of the rotations. In one block of trials, participants were either provided full vision or a verbal description of the laboratory prior to each non-visual rotation ("Preview" condition). In another block, participants were not allowed vision prior to each rotation for the entire block of trials ("No-Preview" condition). Results showed that memory of the environment, whether constructed from visual previews or spatial language, facilitates angular path integration by enhancing the processing of idiothetic self-motion signals (Arthur et al., 2007, 2009). Interestingly, our findings suggest that this increased certainty plays a relatively small role in decreasing systematic errors in self-motion updating. In sum, these findings clearly show that spatial memory can have a robust effect on the precision of path integration.

Our current interest regards exploring the boundary conditions under which spatial memory facilitates path integration. We have argued that the effects of spatial memory on the precision of angular path integration likely stem from the enhanced integration of self-motion signals. In this view, stored spatial representations act as a contextual framework against which incoming vestibular signals are assessed and integrated. Theoretically, all spatial orientation and navigation tasks can be guided by reference to internal spatial frameworks. However, it is apparent that not all tasks require the use of such strategies, and thus a comprehensive understanding of the full impact of stored spatial knowledge on angular path integration remains unclear. Our hypothesis in the current paper is that this benefit is not automatic or obligatory, but instead primarily occurs in orientation tasks in which one's self-location estimate must be referenced to external space (e.g., pointing to a memorized target location or returning to the origin). In contrast, if a task does not explicitly require that participants reference their response to a remembered target location external to the body, spatial memory may not be as beneficial for updating. For example, if participants are required to indicate the magnitude of a body rotation relative to a frame of reference centered on their own body, the external environment is irrelevant to the task, and thus participants may be less inclined to maintain and use the remembered spatial framework to keep track of their orientation during the body rotation. Elucidating the boundary conditions under which spatial memory facilitates path integration is important to not only spatial cognition research, but also to clinical testing of vestibular-deficient patients, and animal vestibular research.

Manipulating the response mode in an angular path integration task provides a means of testing this idea. A strong prediction is that exocentric-referenced responses should show enhanced response precision when previews of the environment are provided prior to the path integration task, while egocentric-referenced responses should not show a preview benefit. In Experiment 1, we tested this prediction by comparing the exocentric-referenced manual pointing response used in our past work (Arthur et al., 2007, 2009) against egocentric-referenced verbal estimates of rotation magnitude (in which there was no requirement to respond relative to a location in the environment). In Experiment 2, we compared egocentric-referenced verbal estimates against an *egocentric*-referenced version of the manual pointing task. Here, as predicted, neither response showed a benefit of preview. In our past work, we showed that response precision in an exocentric pointing task was enhanced even when the remembered spatial framework thought to underlie the preview benefit was specified by spatial language, rather than by vision (Arthur et al., 2009). In Experiment 3, we show that this benefit of remembering a spatial framework disappears when an egocentric pointing response is used, suggesting that one's frame of reference is tightly coupled with sensory integration processes during self-motion updating.

2. General methods

2.1. Materials and apparatus

All experiments were conducted in a laboratory approximately 6 m². Participants were seated in a motorized chair surrounded by a round table 0.80 m high and 1.52 m in diameter, with a circular hole 0.80 m in diameter in the center (see Arthur et al., 2009 for illustration). The table was encircled by a heavy black Polyester curtain (2.55 m high and 3.0 m in diameter). A pointing device was mounted on the arms of the chair immediately in front of participants, at waist level in the horizontal plane. The rotation axis of the pointer was offset from the chair axis by approximately 23 cm; at this offset, the near edge of the pointing device was within a few centimeters of the abdomen for most participants. The pointer itself was a thin rod 16 cm long centered on a polar scale graduated to the nearest degree. The experimenter controlled the acceleration, peak velocity, and total angular displacement of the motorized chair and collected pointer readings with a nearby computer. The chair was mounted to a high-precision rotary stage, the characteristics of which have been described in a previous paper (Arthur et al., 2007). All rotations entailed an accelerating portion of 45°/s², up to a peak velocity of 45°/s, followed by a decelerating portion at 45°/s² down to a full stop. For rotation magnitudes above 40°, the velocity remained constant briefly at 45°/s before the decelerating portion. These parameters ensured that all rotations were well above sensory threshold, with a clearly perceptible beginning and end. Graphical depictions of the velocity profiles generated using this apparatus may be found elsewhere (Arthur et al., 2007).

2.2. Analyses

The rotation axis of the pointer was offset from the vertical axis passing through the center of the chair by approximately 23 cm. Given that the pointer was offset slightly from the chair center, this meant that an accurate response for a body rotation of 90° (defined relative to the chair center) would be 106° (as measured by the pointer). The body rotations were defined relative to the center of the chair, while pointing responses were centered on the pointer axis. To calculate and compare errors between the two reference frames, we adopted the convention of expressing body rotations and pointer responses in the same, chair-centered coordinate system. Prior to analyses, pointing responses were converted to consider this

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