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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, nonvisual 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.

Keywords

spatial memory; path integration; vestibular navigation; manual pointing; perception and action

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

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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, 2002). *Angular path integration* is a special case of path integration, specifically involving updating during angular self-motion (Loomis et al., 1993; Loomis, Klatzky, Golledge, & Philbeck, 1999). 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, “higherlevel” (non-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 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.

General Methods

Materials and Apparatus

All experiments were conducted in a laboratory approximately 6 m square. 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 $45^\circ / \text{sec}^2$, up to a peak velocity of $45^\circ / \text{sec}$, followed by a decelerating portion at $45^\circ / \text{sec}^2$ down to a full stop. For rotation magnitudes above 40° , the velocity remained constant briefly at $45^\circ / \text{sec}$ 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).

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 chair-centered direction. This has the value of facilitating comparisons between body rotations and responses, and comparisons between response types (verbal vs. pointing). Previous research using this paradigm (Arthur et al., 2008) revealed that analyses on the error data using pointing errors calculated relative to the pointer-centered reference frame and pointing errors calculated relative to the chair-centered reference frame differ in only minor ways.

Prior to analyses it was clear in some cases individual responses fell far outside the range of others generated by the participant in similar trials. To identify these responses, we took the absolute value of each raw response for a particular condition. If two responses in the same condition differed by more than 50 deg, we omitted the response that was farthest from the nominal value.

The data were analyzed in terms of two types of error: (1) Variable error, as measured by the within-subject standard deviations across repetitions within a condition. This provides a measure of response consistency, with high error indicating low consistency and vice-versa. (2) Constant error (or “bias”), calculated as the response value minus the physical body rotation magnitude. This provides a measure of the overall tendency to overshoot or undershoot the physically accurate value. Our hypothesis is that spatial memory acts to enhance the precision of path integration. As such, variable error was the main measure of interest.

In the preliminary analyses, circular statistics were used to characterize the central tendencies and dispersions. The circular central tendency and dispersion measures yielded highly similar values to the linear means and standard deviations. Therefore, circular analyses were not further pursued. Instead, we will only report the results of the linear analyses.

To analyze the verbal and pointing errors, repeated measures analyses of variance (ANOVAs) were conducted, with the Viewing Context (Preview / No Preview), Rotation Magnitude (40° , 80° and 140°), and Response Mode (Pointing / Verbal) as *within-subject*

factors and block order (Verbal Mode / Preview, Verbal Mode / No-Preview, Pointing Mode / Preview, and Pointing Mode / No-Preview) being a *between-groups* variable. Separate ANOVAs were performed on the constant and within-subject variable errors. An alpha-level of 0.05 was adopted for all statistical tests.

Experiment 1: Verbal Report versus Exocentric Pointing

Experiment 1 investigated whether one's frame of reference plays a role in the usefulness of previews on the precision of self-motion updating. We predicted that the previously observed benefit of visual preview to the integration of self-motion signals during whole-body rotations will only be manifested in the within-subject precision of the exocentric pointing responses. This prediction stems from the hypothesized difference in the frame of reference underlying these response types.

Method

Participants—Seventeen participants (10 women and 7 men, average age= 19.8, range 18 to 25 years) were recruited to participate in exchange for class credit. All but 3 were right handed. (One additional participant's responses contained numerous conspicuous outliers, suggesting that he or she did not fully understand the pointing instructions. This participant's data were therefore discarded prior to analyses.)

Design—This experiment employed a within-subject randomized block design. There were four blocked within-group conditions: *Verbal Mode / Preview*, *Verbal Mode / No-Preview*, *Pointing Mode / Preview*, and *Pointing Mode / No-Preview*. Block order was fully counterbalanced. Three possible rotation magnitudes of 40°, 80° and 140°, all counterclockwise, were measured 8 times apiece in random order. To broaden the range of rotations, randomly interspersed with these trials were several filler trials involving counterclockwise body rotations of 25°, 55°, 70°, 100°, 115° and 145°, measured two times apiece, for a total of 36 trials. We did not analyze responses from these filler trials because the small number of repetitions provides a poor basis for estimating within-subject response precision, which was our primary focus. Trials were blocked by response mode, with half of the participants using verbal reports first and the other half using pointing first. Within each response mode block, the trials were further blocked by viewing context, resulting in four possible context block orders. Each participant's context block order was repeated between verbal and pointing trials. Within each combination of response mode and viewing context, trials were randomized. We did not analyze for block order effects. Although such analyses can be informative (e.g., Kelly & McNamara, 2008), they can be difficult to interpret without additional experimentation, and a systematic investigation of this issue was not a primary goal of the experiments presented here. Nevertheless, because we were sensitive to the possibility of block order effects, we counterbalanced the block orders, thereby ensuring that any block order effects would be distributed equally amongst the other conditions.

Procedure—In general, the procedure for Experiment 1 was nearly identical to the procedure used in our previous study (Arthur et al., 2009). Participants were individually tested in one session, lasting no more than 60 minutes. Participants donned black-frosted goggles containing circular holes in front of each eye (approximately 2 cm in diameter). The goggles permitted vision of a head-fixed light (HFL) but prevented vision of any light inadvertently leaking in from the surrounding environment. The HFL consisted of a single light-emitting diode (LED) presented at eye-level and at a distance of approximately 0.55 m from the participant's head, and remained fixed relative to the participant's head during body rotations. This HFL served to minimize the vestibular-ocular reflex (VOR) and other variations in ocular behavior between participants. In addition, a vertically- and

horizontally- adjustable cushioned headrest was mounted onto the back of the chair and served as a head restraint. At the beginning of each Preview trial, participants raised the goggles and viewed the surrounding environment for several seconds. After this preview, the overhead lights were extinguished, and participants were instructed to don the goggles and to fixate the HFL. Although we did not measure eye movements, we had no a priori reason to suspect that participants would not comply with the fixation instructions. They received a verbal warning and then a passive body rotation in darkness. Participants underwent one of the possible stimulus rotations. After a 5 sec delay, which allowed the semicircular canal fluids to settle, participants were cued (by extinguishing the HFL) to give their verbal or pointing estimate of the origin location (still without vision and without receiving error feedback). After the response was recorded, participants were rotated back to the starting orientation (0°), using the same velocity profile as during the stimulus phase, to begin the next trial. In the Preview block, participants raised the goggles and viewed the surrounding environment for several seconds prior to the next trial. After this preview, the lights were extinguished, and participants were instructed to don the goggles and to fixate on the HFL. They then received a verbal warning prior to the passive body rotation in darkness. In the No-Preview block, prior to the experimental trials participants were disoriented with respect to the surrounding environment by administering a series of clockwise and counterclockwise whole-body rotations ranging between 40° and 200° (see Arthur et. al, 2007 for more details). The procedures in No-Preview trials employed the same rotation magnitudes and were nearly identical to Preview trials, except here, participants remained in the dark throughout the entire block of the trials.

Verbal Trials: Participants were instructed to respond using the egocentric location of the origin in degrees coupled with an indication of direction (e.g., “90 degrees to the right”). Participants were also instructed to be as precise as possible, and were encouraged to use increments of 5 degrees or less. After the response was recorded participants were rotated back to the starting orientation (0°), using the same velocity profile as during the stimulus phase, to begin the next trial.

Pointing Trials: These trials involved exocentric-referenced pointing responses. Here participants were informed of the offset of the pointer’s axis relative to the chair’s axis and were instructed to point so that an imaginary line would extend from the pointer and connect directly to the origin location. To demonstrate the meaning of this instruction, they were shown that for a body rotation of 90° , simply setting the pointer to 90° was inaccurate because the pointer would not point directly to the location of the origin, due to the offset of the pointer from the chair center (see General Methods). Participants were asked to consider the origin to be a specific location on the circular perimeter of the table, rather than a general direction with no definite distance.

Results

Prior to analyses, twenty-four data points were identified as within-subject outliers and were omitted according to the rule described above (see General Methods). This resulted in the removal of less than 2 % of the data.

Variable Error—We assessed *within-subject* variable error by calculating within-subject standard deviations across four measurements per condition.

An ANOVA showed a significant effect of Response Mode ($F[1, 16] = 6.763$; $p = .019$); pointing responses tended to be a bit more variable than verbal responses overall (see Figure 1a): the mean variable error across conditions was 13.8° and 11.2° , respectively. There was an effect of Viewing Context ($F[1, 16] = 8.052$; $p = .012$), with standard deviations being

reliably higher in No-Preview than in Preview conditions (averaging 14.4° vs. 10.7° , respectively). This effect was qualified by a significant interaction between Viewing Context and Response Mode ($F[1, 16] = 4.998$; $p = .042$). Importantly, pairwise planned contrasts revealed that this effect was entirely due the pointing responses ($p < .05$); there was no reliable difference between the Preview and No-Preview condition for the verbal responses ($p < .05$). There was also a main effect of Rotation Magnitude ($F[2, 32] = 9.00$; $p = .001$). The mean variable errors across context for the 40° , 80° , and 140° body rotations were 8.24° , 9.66° , and 15.83° for the verbal responses and 10.90° , 13.42° , and 11.39° for the pointing responses, respectively. There were no other significant interactions (Rotation Magnitude $\times$ Viewing Context ($F[1, 16] = 2.556$; $p = .129$); Response Mode $\times$ Rotation: $F[2, 32] = 0.283$; Context $\times$ Rotation: $F[2, 32] = .636$; Response Mode $\times$ Rotation $\times$ Context: $F[2, 32] = 1.435$; all p 's $> .05$).

The Response Mode $\times$ Rotation $\times$ Context interaction was not reliable, and thus, strictly speaking, post-hoc comparisons at a fine-grained level are not appropriate. Nevertheless, we were struck by the apparent lack of a Viewing Context effect for pointing responses with 140° rotations (see Figure 1a). As a rough test of this, we compared Preview and No-Preview conditions for each rotation magnitude. For pointing responses, one-tailed t-tests showed that there was a significant preview effect for the 40° and 80° rotations (both p 's $< .022$), but not for the 140° rotations ($p = .096$). Similar analyses for verbal responses showed no effect of preview at any rotation magnitude (all p 's $> .244$).

Constant Error—The mean constant (signed) errors are plotted in Figure 1b. An ANOVA on the constant errors showed that there was no effect of response mode ($F[1, 16] = 1.917$; $p = .185$). The mean constant errors were 3.07 and -2.38 for the verbal and pointing response, respectively. There was no effect of Viewing Context ($F[1, 16] = .824$; $p = .377$). The mean constant error in Preview trials was -1.1° , versus 1.8° in the No-Preview trials. There was no effect of Rotation Magnitude ($F[2, 32] = .385$; $p = .683$): the mean errors for 40° , 80° and 140° rotation trials were 0.72° , 1.56° and -1.25° , respectively. However, there was a Response Mode $\times$ Rotation interaction ($F[2, 32] = 5.564$; $p = .008$). Verbal responses slightly overestimated the 80° and 140° rotation magnitudes, whereas pointing responses tended to *undershoot* the same rotations. There were no other significant interactions (Response Mode $\times$ Context: $F[1, 16] = .179$; Context $\times$ Rotation: $F[2, 32] = 1.469$; Response Mode $\times$ Rotation $\times$ Context: $F[2, 32] = .191$; all p 's $> .05$). The mean constant errors across context for the 40° , 80° , and 140° body rotations were -1.25° , 5.70° , and 4.76° for the verbal responses, and 2.69° , -2.58° , and -7.25° for the pointing responses, respectively.

Discussion

Our primary predictions centered on the *within-subject variability* in comparing pointing responses that were exocentric-referenced, in that they were explicitly directed to remembered locations external to the body, and verbal reports, which were presumably egocentric-referenced, in that they did not require reference to an external location. As expected, we found a significant effect of response measure on the variable errors. There were no reliable differences between the constant errors for pointing and verbal responses, however. This confirms that benefit of this preview to the integration of self-motion signals is manifested in terms of variable error. Overall, the standard deviations of verbal reports were significantly lower than pointing response. Importantly, post-hoc analyses showed that this effect was solely due to the No-Preview trials. Results revealed that not having access to a visual preview of the surrounding environment prior to angular displacement in the No-Preview trials led to an approximate 55.5% increase in variable error as compared to the Preview trials (10.8° vs. 16.8° , respectively) in the exocentric pointing trials. However, this observed effect of previews on the precision of pointing responses disappeared when using

verbal report. Further tests showed no effect of preview at the large rotation (140°) for pointing responses (see Figure 1a). Although the reason for this result is unclear, it is possible that participants used a more egocentric strategy when pointing for the large rotation, thereby benefitting somewhat less from the preview. This result may be spurious, however, as we typically have observed a robust preview effect for pointing responses at similar rotation magnitudes in our past work (Arthur et al., 2007; 2009) under highly similar conditions (see also the results of Experiment 2, below). Regardless, as predicted, we found that there was no significant difference between the within-subject variability of the Preview and No-Preview trials for verbal responses. Taken together, these results suggest that knowledge of the spatial layout may only be effective when using an exocentric-reference response. We further investigated this issue in Experiment 2.

Experiment 2: Verbal Report versus Egocentric Pointing

Results for Experiment 1 suggest the usefulness of spatial memory in the precision of self-motion updating may be tightly linked to one's frame of reference. Our experimental instructions specified that verbal responses should indicate an estimate of the origin location relative to straight ahead—and it is reasonable to assume that straight ahead is typically egocentrically referenced. However, it is possible, though unlikely, that participants could have made the judgment relative to some other reference. The current experiment further investigated whether the effect of response mode found in Experiment 1 was in fact due to the frame of reference underlying the responses. Verbal reports and *egocentric* pointing responses were collected. Participants were now given a new set of instructions using the same pointing apparatus (thus keeping the motoric requirements the same): participants were explicitly told to adjust the pointer to *reproduce* the magnitude of the stimulus rotation relative to their body. If some aspect of the frame of reference underlying the response plays a role in the integration of vestibular signals, then egocentric pointing should now closely resemble verbal reports in showing no benefit of visual previews, presumably because information about the external environment is no longer strictly required for the task. We predicted that the previously seen benefit of visual preview on manual pointing responses should disappear since participants would no longer be using an exocentric-referenced response.

Method

Participants—Twenty-four participants (12 women and 12 men, average age= 19.2, range 18 to 21 years) were recruited to participate in exchange for class credit. One participant was left-handed.

Design—This experiment employed within-group and between-subject randomized block designs. There were two blocked within-group conditions: *Verbal Mode* and *Pointing Mode* and two between-group conditions: *Preview* and *No Preview*. Participants were individually tested in one session lasting no more than 60 minutes. As in the previous experiment, response mode and rotation magnitude were varied within subjects. Trials were blocked by response mode, with half of the participants using verbal reports first and the other half using pointing first. Trials were randomized within each block of verbal and pointing mode. The same rotation magnitudes and filler stimulus rotations from Experiment 1 were used. Again, we did not analyze for block order effects.

Procedure—The following experiment did not use the HFL or head restraint as in Experiment 1, as previous studies show that results are similar when eye movements were not restricted during the body rotations (Arthur et al., 2007). Here, participants donned

black-frosted goggles that prevented vision of any light inadvertently leaking in from the surrounding environment.

Verbal Trials: These trials were identical to those used in Experiment 1.

Pointing Trials: The pointing trials were nearly identical to those used in Experiments 1, except here participants were specifically instructed to use the pointer to indicate the magnitude of the stimulus rotation. In addition, participants' understanding of the instructions was verified by conducting a "practice" rotation. In this practice rotation, participants raised the blindfold and were rotated 90° counterclockwise and then instructed to use the pointer to indicate their response as previously described. This practice trial provided participants with visual feedback during the rotation and as they used the pointer to *reproduce* the 90° stimulus rotation with the pointing device.

Results

Variable Error—We assessed within-subject variable error by calculating within-subject standard deviations across seven measurements per condition. An ANOVA showed a significant effect of Rotation Magnitude ($F[1,23] = 12.779$; $p = .002$). The mean variable errors across context and response mode for the 40°, 80°, and 140° were 8.87°, 14.93°, and 18.5° respectively. There was no effect of Response Mode ($F = 1.368$; $p = .255$). The mean variable errors across context for the 40°, 80°, and 140° body rotations were 9.1°, 17°, and 18.6° for the pointing responses and 8.75°, 12.85°, and 18.4° for the verbal responses, respectively (see Figure 2a). In addition there was no effect of Viewing Context ($F = 2.354$; $p = .139$) with standard deviations averaging 15.32° in the No Preview condition and 12.92° in the Preview condition. There were no significant interactions found (Response Mode $\times$ Rotation Magnitude: $F = 1.131$; Response Mode $\times$ Viewing Context: $F = .048$; Rotation Magnitude $\times$ Viewing Context: $F = .677$; Response Mode $\times$ Rotation Magnitude $\times$ Viewing Context: $F = .687$; all p 's $> .05$).

Constant Error—The mean signed errors are plotted in Figure 2b. An ANOVA on the constant errors showed that there was a significant effect of Rotation Magnitude ($F = 433.163$; $p < .001$): the mean errors for 40°, 80°, and 140° rotation trials were -5.32° , -6.03° , and -2.28° , respectively. There was no effect of Response Mode ($F = .282$; $p = .601$). The overall mean constant errors were -3.55° and -5.53° for the verbal and pointing response, respectively. There was no effect of Viewing Context ($F = 1.151$; $p = .295$). The overall mean constant error in Preview trials was -8.17° and -92° in the No-Preview trials. There were no significant interactions (Response Mode $\times$ Rotation Magnitude: $F = .934$; Response Mode $\times$ Viewing Context: $F = 1.836$; Rotation Magnitude $\times$ Viewing Context: $F = .058$; Response Mode $\times$ Rotation Magnitude $\times$ Viewing Context: $F = .901$; all p 's $> .05$).

Discussion

Experiment 2 was designed to further investigate the source of the effect by collecting *egocentric* pointing responses in addition to verbal responses. It was predicted that the previously seen benefit of visual previews should disappear since participants would no longer rely on an exocentric reference frame. The results of Experiment 2 supported our predictions. We found that when participants were now required to generate egocentric pointing responses, the effect of context disappeared. In addition, the previous advantage of verbal responses over pointing responses seen in Experiment 1 disappeared; there was no effect of response mode in terms of accuracy or precision.

These results support the frames of reference hypothesis, or the idea that the frame of reference underlying the response measure significantly influences angular self-motion updating. This issue is further discussed in the *General Discussion* section.

Experiment 3: Imagined Previews and Angular Path Integration

Experiment 2 confirmed that spatial memory is a powerful input to exocentric-based self-motion updating tasks. We recently began an investigation into what aspects of a remembered environment play a role in eliciting enhanced angular path integration. This enhancement may only occur when a certain level of visual detail is present in the external environment. In contrast, relatively little detail may be sufficient to elicit similar benefits. We previously found that the precision of angular path integration is significantly enhanced even when participants were provided with relatively little detail from “imagined previews” before the whole-body rotations (Arthur et al., 2009). In that experiment, we contrasted the No-Preview condition with a more controlled Preview condition, in which the “preview” was an imagined environment defined purely by spatial language. Results showed that the standard deviations were substantially lower in the Imagined Preview trials (by approximately 82 %) than in the No-Preview trials. These findings suggest that stored spatial representations gained from spatial language are functionally equivalent to those gained from direct visual previews, acting to enhance angular path integration by decreasing uncertainty in participants’ self-location estimates. Exocentric pointing was the response mode in our previous work. If our hypothesis is correct that spatial memory enhances path integration specifically in tasks requiring participants to update relative to an external frame of reference, a strong prediction is that the previously found benefit of “imagined previews” should disappear when *egocentric* -pointing responses are used, and in fact the pointing responses should now be more similar to the verbal responses, which presumably are also egocentric-referenced. In Experiment 3, we tested this idea.

Method

Participants—Twenty-eight participants (20 women and 8 men, average age= 19.2, range 18 to 22 years) were recruited to participate in exchange for class credit. All but three of the participants were left-handed.

Design—This study used the same design as in Experiment 2.

Procedure

Imagined Preview Condition: Subjects in the preview condition performed the experiment exactly the same as in Experiment 2, except here an imagined preview was used.

Learning Phase: Participants first took part in a learning phase where the experimenter described the positions of four objects in the environment by specifying their egocentric directions and distance (e.g., “desk, 3 o’clock, 5 feet”). Four familiar objects were selected: a chair, desk, computer, and filing cabinet. Participants were told to “get a clear image in your mind of where each of the imagined objects is located” to encourage them to encode these egocentric relations into a spatial image instead of merely creating a verbally based representation. Objects locations were distributed in four directions corresponding to the intrinsic axes of the body, with no two objects at the same direction. After describing the objects’ locations the experimenter tested participants’ knowledge of the object locations by presenting them with the names of the objects in random order. After hearing the object’s name participants aimed the pointer towards the imagined object. The learning phase continued until absolute pointing errors were less than 10°. This learning phase ensured that participants encoded the layout described by spatial language.

Experimental Phase: The experimental phase for the *Preview Condition* was almost identical to the one used in Experiment 2, except participants were not allowed to view the environment prior to each trial. Instead, they were instructed to “get a clear image in mind of where each of the imagined objects is located,” prior to each body rotation. The procedures used in the *No-Preview Condition* were identical to those used in the No-Preview trials in the previous experiments.

Results

Variable Error—We assessed within-subject variable error by calculating within-subject standard deviations across seven measurements per condition. An ANOVA showed a significant effect of Rotation Magnitude ($F = 27.206$; $p < .001$). The mean variable errors across context and response mode for the 40°, 80°, and 140° were 8.39°, 12.42°, and 19.31° respectively. There was no effect of Response Mode ($F = .001$; $p = .972$). The mean variable errors across context for the 40°, 80°, and 140° body rotations were 8.03°, 11.91°, and 20.80° for the pointing responses and 8.74°, 12.92°, and 18.54° for the verbal responses (see Figure 3a). In addition there was no effect of Viewing Context ($F = .135$; $p = .716$) with standard deviations averaging 13.14° in the No Preview condition and 13.60° in the Preview condition. There were no significant interactions found (Response Mode $\times$ Rotation Magnitude: $F = .460$; Response Mode $\times$ Viewing Context: $F = .664$; Rotation Magnitude $\times$ Viewing Context: $F = .101$; Response Mode $\times$ Rotation Magnitude $\times$ Viewing Context: $F = 1.526$; all p 's $> .05$).

Constant Error—The mean signed errors are plotted in Figure 3b. An ANOVA on the constant errors showed that there was a significant effect of Rotation Magnitude ($F = 365.707$; $p < .001$): the mean errors for 40°, 80°, and 140° rotation trials were -3.62° , -5.67° , and -3.27° , respectively. There was no effect of Response Mode ($F = 1.013$; $p = .323$). The overall mean constant errors were -2.83° and -5.56° for the verbal and pointing response, respectively. There was no effect of Viewing Context ($F = .015$; $p = .903$). The overall mean constant error in Preview trials was -3.83° and -4.55° in the No-Preview trials. There were no significant interactions (Response Mode $\times$ Rotation Magnitude: $F = 1.666$; Response Mode $\times$ Viewing Context: $F = .283$; Rotation Magnitude $\times$ Viewing Context: $F = .261$; Response Mode $\times$ Rotation Magnitude $\times$ Viewing Context: $F = .028$; all p 's $> .05$).

Discussion

As predicted, when using the egocentric pointing response there was no longer an effect of imagined previews on the precision of manual pointing. These results provide further support to our frames of reference hypothesis. The fact that we were able to replicate the results from Experiment 2 suggests that response mode exerts a robust effect on response precision of angular path integration. Moreover, the absence of an effect of preview (whether visual or imagined) in both the verbal and egocentric pointing responses further supports the notion that the frame of reference underlying the response plays an important role in angular path integration.

General Discussion

A series of experiments was conducted to investigate the source of the effect of previews on the precision of angular path integration using verbal and pointing responses. We found that the benefits of previews (both visual and imagined) on perceived angular displacement disappeared when participants used response measures that were referenced to the body rather than the external environment. These results, together with our previous findings (Arthur et al., 2007, 2009), suggest that memory of a spatial layout is primarily beneficial

for path integration when participants adopt an exocentric frame of reference. When the task encourages participants to call to mind a spatial layout, this provides a spatial framework that facilitates integration of incoming sensory self-motion information. Memory of a surrounding spatial layout is especially relevant when the task requires responses to be referenced to remembered locations external to the body—hence, there is a benefit of previews on path integration when exocentric-referenced responses are used. When egocentric-referenced responses are used, even if a participant calls to mind a spatial layout (based either on a recent visual preview of the surrounding environment or memory of an imagined layout), this memory does not enhance path integration because there is no explicit requirement to link this memory to the on-going self-motion signals.

Our results highlight the importance of response modes in the context of measuring perceived angular displacement. In our paradigm, the stimulus conditions and methods were closely matched between the preview and no-preview conditions, and the verbal and pointing response conditions. The main difference between the verbal and pointing conditions was the frame of reference underlying the response measures, which was varied by instructional manipulations. However, verbal and pointing responses differ along multiple dimensions. One major difference is the mechanical output: pointing responses are action-based responses, in that they require a complex set of perceptuomotor transformations (i.e., retinocentric coordinates of the visually acquired target translated into a set of specific motor commands, see Soechting & Flanders, 1992), while verbal responses are non-action-based as they do not require such complex transformations. This is an important distinction as pointing responses could potentially be biased by the mechanical constraints and physical properties of the arm and hand. However, in our paradigm, the same pointing device was used in both preview conditions (visual/spatial language vs. no previews). In addition, the presence or absence of previews was manipulated within-subjects, thus there should be no differences in terms of how the pointer is used between conditions. Another difference between manual pointing and verbal responses is that verbal responses must be produced in discrete units (e.g., degrees), whereas manual pointing allows for a more continuous range of responses (see Philbeck et al., 2008 for more details on the distinction between verbal and pointing responses). In our paradigm, we instructed participants to be as precise and accurate as possible when giving verbal estimates. On average, participants complied with using small verbal units. Therefore, the increased response precision is unlikely to stem from the above distinctions between verbal and pointing response. Instead, our current data demonstrate another crucial difference between verbal and pointing responses in the context of indications of angular displacement. Specifically, the frame of reference during whole-body rotations has a significant effect on the integration of incoming sensory signals (Israël et al., 2005; Siegler, 2000). In other words, incoming sensory signals during passive whole-body rotations may be directly integrated to yield a perception of self-motion and self-location estimates in egocentric-based terms, and as a result, spatial memory of the external environment is not needed. In contrast, remembered spatial frameworks are useful when using an exocentric frame of reference. This is supported in the increased variability in participants' responses when using an exocentric pointing device in the No-Preview trials.

These data reinforce the notion that there are important individual differences in cognitive strategies during path integration (Israel et al., 2005; Siegler, 2000). In an experimental setting, the methodology might tend to make memory of the surrounding environment less salient (for example, because multiple trials are conducted without visual input, allowing the spatial memory to decay). The precision of path integration could be significantly underestimated for individuals tested under these circumstances. The benefit of visual previews is not obligatory, however. The choice of response mode might impact path integration by encouraging individuals to adopt either an egocentric or an exocentric frame

of reference, and conceivably participants might spontaneously choose to adopt one or the other of these reference frames. Our current results show that the combination of visual previews with exocentric-referenced responses dramatically enhances the precision of angular path integration.

Moreover, the enhancement of path integration by internal spatial representations lends support to the growing notion that sensory self-motion signals are not the sole inputs to path integration (Arthur et. al, 2007, 2009; Jürgens & Becker, 2006; Jürgens, Nasios, & Becker, 2003; Tcheang, Bühlhoff, & Burgess, 2011). Instead, cognitive inputs may be combined with incoming sensory signals during angular displacements, resulting in more finely-tuned responses for exocentric-based spatial updating tasks. We previously argued that stored spatial representations, gained from visual and nonvisual modalities, act as a framework that provides a spatial context against which incoming vestibular signals are evaluated and integrated. The present results are consistent with this idea, further establishing that this benefit is specific to exocentric spatial updating tasks. Enhancements in the precision of angular path integration by spatial memory inputs suggest that multiple independent sources of information (sensory and non-sensory) contribute to the perceptual indication of angular displacement. There is no reason to expect spatial memory encoded on the basis of visual previews and spatial language to be the only effective source for enhancing path integration performance. We suspect that remembered spatial frameworks derived from other sensory modalities, such as a tactile “preview”, should also be sufficient to facilitate angular path integration by decreasing the uncertainty of self-location estimates. Similarly, having access to self-motion inputs from multiple sensory modalities (as might happen during more real-world navigation) should not necessarily obliterate the context effects we have shown here. Our view is that the determining factor instead lies in the situational constraints that encourage individuals to reference their updated self-motion to the external environment. Our findings are consistent with others (Anderson, Synder, Bradley, & Xing, 1997; Tcheang, Bühlhoff, & Burgess, 2011), in that multiple sensory inputs may be combined into a single multimodal internal representation of space to guide *exocentric* behavioral responses (e.g., pointing, walking, throwing, etc.).

Neurophysiological studies in animals have identified a variety of vestibular-driven cells, which are thought to be the neural correlates of (angular) path-integration: place cells, head direction (HD) cells, whole-body motion cells, and grid cells (for reviews see Calton & Taube, 2009; Stackman, Golob, Bassett, & Taube, 2003; Taube, Goodridge, Golob, Dudchenko, & Stackman, 1996). The neural process of integrating sensory and non-sensory cues for optimizing angular path integration remains to be explored. One feasible basis by which the facilitation of path integration by spatial memory may occur is via the entorhinal-hippocampal system (Jefferey, 2008). As the main interface between the hippocampus and the neocortical multimodal areas and surrounding parahippocampal gyrus, the entorhinal cortex (EC) has reciprocal connections to the hippocampus (Fyhn, Molden, Menno, Witter, Moser, & Moser, 2004; Jefferey, 2008; Witter & Moser, 2006). The EC is thought to play a vital role in navigation, linking stored conjunctive spatial and non-spatial representations in the hippocampus with multi-sensory inputs for self-localization within one’s immediate environment (Jefferey, 2008). There is evidence that the medial entorhinal cortex (MEC) plays a central role in path integration and spatial memory (McNaughton, Battaglia, Jensen, Moser, & Moser, 2006; Witter & Moser, 2006). Co-located in the MEC are positional grid cells, head direction cells, conjunctive cells (i.e., receiving positional and directional input), border cells and path-equivalent cells (Jacobs, Kahana, Ekstrom, Mollison, & Fried, 2010; McNaughton et al., 2006; Solstad, Boccara, Kropff, Moser, & Moser, 2008). The MEC has received much attention due to the topographically organized grid cells that are modulated by external cues. However, whether the MEC plays a more specialized role in *angular* path integration is unclear (see Clark & Taube, 2011). We suspect that the entorhinal-

hippocampal system may provide a substrate with which incoming sensory information and non-sensory inputs, such as visual imagery, converge to form a supramodal spatial representation of one's current orientation in the immediate environment. Additional neurophysiological and neuroanatomical studies of the EC in animals and humans are needed to test this hypothesis.

In sum, our work provides a clearer understanding of the conditions under which higher-level (cognitive) processes contribute to self-motion updating, specifically angular path integration. Our findings are relevant to physiological, neuropsychological, and neuroimaging studies on the neural substrates of spatial orientation and navigation, and the development of computational models of human path integration. The powerful role of spatial memory in path integration has significant methodological implications for future studies assessing participants' perception of whole-body rotations. Also, these findings may be extended beyond the laboratory and applied to spatial navigation training in virtual environments and clinical navigational testing in vestibular patient populations.

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Research Highlights

- We examined the conditions under which spatial memory facilitates path integration
- Administered passive, non-visual body rotations about the yaw axis
- Compared verbal report and manual pointing to indicate magnitude of the rotation
- The powerful effect of spatial memory is dependent on one's frame of reference

A)

B)

Figure 1.

(A) Mean within-subject standard deviation in each condition, calculated across participants, and (B) mean constant (signed) error in each condition, calculated across participants in Experiment 1. Error bars denote $\pm$ one standard error of the mean.

A)

B)

Figure 2.

(A) Mean within-subject standard deviation in each condition, calculated across participants, and (B) mean constant (signed) error in each condition, calculated across participants in Experiment 2. Error bars denote $\pm$ one standard error of the mean.

A)

B)

Figure 3.

(A) Mean within-subject standard deviations in each condition, calculated across participants, and (B) Mean constant (signed) error in each condition, calculated across participants in Experiment 3. Error bars denote $\pm$ one standard error of the mean.