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RESEARCH ARTICLE

Rotational error in path integration: encoding and execution errors in angle reproduction

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Abstract Path integration is fundamental to human navigation. When a navigator leaves home on a complex outbound path, they are able to keep track of their approximate position and orientation and return to their starting location on a direct homebound path. However, there are several sources of error during path integration. Previous research has focused almost exclusively on *encoding error*—the error in registering the outbound path in memory. Here, we also consider *execution error*—the error in the response, such as turning and walking a homebound trajectory. In two experiments conducted in ambulatory virtual environments, we examined the contribution of execution error to the rotational component of path integration using angle reproduction tasks. In the reproduction tasks, participants rotated once and then rotated again to face the original direction, either reproducing the initial turn or turning through the supplementary angle. One outstanding difficulty in disentangling encoding and execution error during a typical angle reproduction task is that as the encoding angle increases, so does the required response angle. In Experiment 1, we dissociated these two variables by asking participants to report each encoding angle using two different responses: by turning to walk on a path parallel to the initial facing direction in the same (reproduction) or opposite (supplementary angle) direction. In Experiment 2, participants reported the encoding angle by turning both rightward and leftward onto a path parallel to the initial facing direction, over a larger range of angles. The results suggest that execution error, not encoding error, is the predominant source of error in angular path integration. These findings also imply that the path integrator uses an intrinsic (action-scaled) rather than an extrinsic (objective) metric.

Keywords Navigation · Idiothetic · Self-motion · Intrinsic metric · Perception–action · Virtual reality

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Introduction

Path integration is one of the basic mechanisms that humans and other animals use to navigate in their environments. Successful path integration allows a navigator to register the distances and angles they have traversed and take a direct path back to their starting location. Path integration depends on information about self-motion, including *idiothetic* (i.e., proprioceptive, vestibular, and motor) information and *optic flow*. Human path integration has a low resolution compared with many other species (e.g., Müller and Wehner 1988), but it is still quite useful for orienting (Chance et al. 1998; Kearns et al. 2002; Klatzky et al. 1990; Loomis et al. 1993; Peruch et al. 1997; Zhao and Warren 2015a, b) and contributes to the acquisition of survey knowledge (Chrastil and Warren 2013; Wang 2016).

One outstanding question about path integration is whether the underlying metric is intrinsic or extrinsic. An intrinsic metric measures distances and angles in embodied action-scaled units specific to the actions involved, such as stride lengths, rotation velocities, or joint angles. In contrast, an extrinsic metric measures absolute distances and angles in objective units such as meters or degrees that are independent of the navigator. An extrinsic metric could potentially facilitate metric conversion across modalities, such as when walking and throwing the same distance. We have recently reported that, for the translational component of path integration, the human odometer registers distances in an intrinsic metric (Chrastil and Warren 2014). Here, we ask whether, for the rotational component, the human path integration system similarly registers angles in an intrinsic, body-based metric during locomotion.

Another outstanding question is the source of the systematic errors observed in path integration. Three potential sources of systematic error have been identified (Fujita et al. 1993; Loomis et al. 1993), including (1) *Encoding* the distances and angles on outbound path, (2) *Integrating* this information to determine the direct homebound path, and (3) *Executing* the homebound path, which requires turning through the intended angle and traveling the intended distance to the starting location. It is possible for error to accumulate during any of these processes. The purpose of this study is (1) to determine whether the path integrator registers angles in an intrinsic metric and (2) to disentangle the encoding and execution errors in angle reproduction tasks.

A well-known model of path integration proposes that the largest source of systematic error lies in encoding the outbound path (Fujita et al. 1993). The aptly-named encoding-error model assumes that integrating the information to determine the homebound path and executing that path contribute no systematic error to path integration, although random error could occur at any stage. The assumption of no systematic execution error stems from accurate performance in blindfolded walking to target paradigms (e.g., Loomis et al. 1992; Thomson 1983), while the assumption of no systematic integration error suggests that humans have an internal computational process akin to "cognitive trigonometry" or the ability to measure distances and angles from a mental image (Fujita et al. 1993). Most subsequent tests of path integration have also discounted errors due to integration and execution (e.g., Benhamou and Seguinot 1995; Klatzky et al. 1999). Evidence of systematic integration or execution errors in path integration would entail revising these path integration models.

While some studies have shown little error in execution of a planned trajectory (Jürgens et al. 2003; Riecke et al. 2002), others have demonstrated significant bias in the simple production of canonical angles (Bakker et al. 1999, 2001; Israel et al. 1995; Klatzky et al. 1990). These production errors did not require encoding the angle through movement, but rather simple execution of a cardinal angle, suggesting a contribution of execution error. For example, Bakker et al. (1999, 2001) showed that production errors for verbally specified turns of 90°, 180°, or 270° ranged from approximately 5°–45° in conditions with the most sensory information, and from approximately 20°–120° in a purely visual task. In addition, several of these studies have found evidence that reproducing an angle may lead to lower errors than executing one (Israel et al. 1995; Klatzky et al. 1990). This result supports an intrinsic metric, because it may be easier to reproduce intrinsic information than to produce a specified extrinsic angle.

Other researchers have also found that reproducing a rotation is fairly accurate, although there is a robust finding of a tendency to overturn small angles and underturn large angles (Becker et al. 2000; Israel et al. 1996; Israël and Warren 2005, for a review) Ivanenko et al. 1997; Jürgens et al. 2003; Klatzky et al. 1997; Loomis et al. 1993; Marlinsky 1999; Metcalfe and Gresty 1992; Sadalla and Montello 1989; Siegler 2000; Siegler et al. 2000; Vidal and Bülthoff 2010; see). However, angle reproduction tasks possess one key problem when attempting to distinguish encoding and execution error: as the outbound turn angle increases, the required response angle also increases. If errors tend to increase as the outbound angle increases, it is possible that the errors also stem from the increased demands upon the *execution* of the response. In simple angle reproduction, there is no integration error from combining multiple angles and path lengths. Executing a response could involve several sources of error: monitoring self-motion, maintaining the desired target location in memory, comparing desired movement with actual movement, or a misfire of efferent motor commands.

This study aims to test two models of path integration error: (1) the encoding-error model, which predicts that systematic errors are due solely to errors in encoding, regardless of the required response and (2) an alternative model that predicts that systematic errors could also stem from executing the response. To distinguish encoding and execution errors, the response angle must be dissociated from the encoding angle, meaning that angle reproduction alone will not suffice. The experiments presented here isolate encoding and execution errors by requiring participants to respond to the same initial turn angle in two different ways. In the first experiment, participants walked down a main hallway in a virtual environment, turned into a branching hallway, and were then instructed to turn and walk parallel to the main hallway, either continuing in the original direction or walking in the opposite direction. In the second experiment, participants were instructed to turn both leftward and rightward in these two tasks, over a wider range of angles. This design predicts similar response patterns if all error is due to encoding, but different patterns if some error is due to execution.

Experiment 1

Methods

Participants

Seven female and eight male volunteers were paid for their participation in this study. One female and one male withdrew due to symptoms of simulator sickness. Ages of the remaining 13 participants ranged from 19 to 30 (mean 25.73). All participants signed forms indicating their informed consent to be a part of the study in fulfillments of the requirements of the Brown University IRB.

Equipment

Participants walked freely in a 12 × 12-m tracking area while wearing a head-mounted display (HMD), in the VENLab. The participant viewed a virtual environment in a Cybermind Visette 2 HMD (60° H × 46.8° V field of view, 640 × 480 pixels, 60 Hz frame rate), and wore a backpack containing some cables, which weighed approximately 3 pounds and did not impede movement. Head movement was recorded using an InterSense IS900 tracking system (60 Hz sampling rate, 1.5 mm RMS and 0.1° RMS accuracy) and used to update the display (50 ms latency). Participants made responses with a USB radio mouse. The virtual environment was generated on a graphics PC (Alienware, NVIDIA Quadro FX 3000 graphics card) using the Vizard software (WorldViz) to render the images. Naturalistic cricket sounds, instructions, and cues to start and stop walking were presented to the participants over headphones.

Procedure

This experiment was conducted in two sessions. In each session, participants were given instructions, walked in a practice environment, and performed four practice trials for 5–10 min, sufficient time to adapt to virtual reality (Mohler et al. 2006). The instructions were repeated before the start of the experiment. Test trials were then presented in one block, with frequent opportunity for breaks. Each session lasted 40–60 min.

This experiment was conducted as part of a larger study that included a total of five sessions over the course of 2–6 weeks. The conditions reported here were presented in two counterbalanced sessions during sessions 3–5 of the larger study. Typically, each participant received one session every 4 days; there was a break of at least 4 h between sessions.

Tasks

The participant began each trial by walking down a virtual hallway (Fig. 1a; 1 m wide, 100 m long, leaf texture on the walls and gravel texture on the ground) until an auditory cue indicated that they should stop, approximately 5.86 m from the start. The hallway then disappeared and was replaced by a cylindrical hedge surrounding the participant (radius 1 m). The participant was instructed to turn right or left until an auditory cue indicated they should stop (within ±3° of 30°, 60°, 90°, 120°, and 150°). The hedge was mapped with a foliage texture that provided optic flow information about the magnitude of the rotation, in addition to idiothetic information. A second hallway at the specified angle then replaced the cylindrical hedge. Participants walked down this hallway until another auditory cue indicated they should stop, and the cylindrical hedge

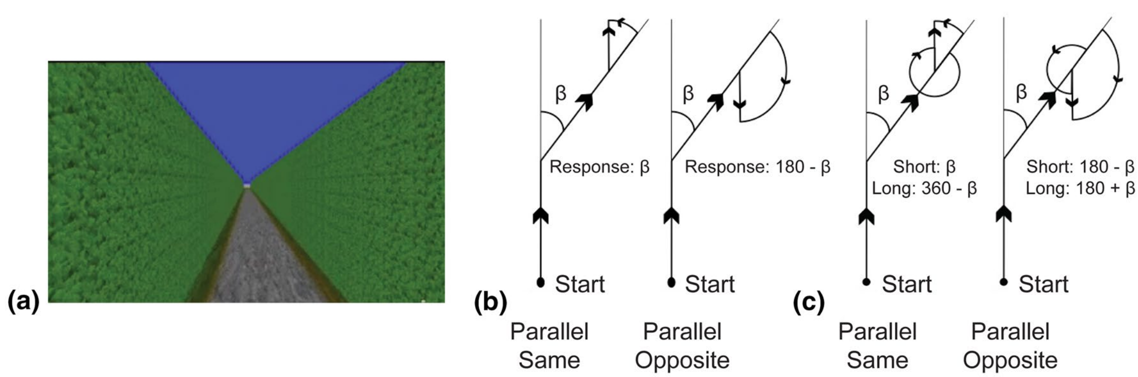

Fig. 1 **a** View of hallway displays seen by participants. **b, c** Overhead view of the experimental tasks. *Large arrowheads* indicate direction of outbound path, and *smaller arrowheads* indicate the turn direction for the correct response. **b** Experiment 1: the arc shows the correct response for the Same and Opposite conditions. **c** Experiment 2: the arc with the greater radius represents the "short" response and the arc with the smaller radius represents the "long" response

reappeared. They were then instructed to turn until they were facing in a direction parallel to the first hallway and click the mouse, whereupon a third hallway opened up in the direction they were facing. After walking forward 1.5 m, the trial ended.

In the Same condition, participants were asked to take a path parallel and in the same direction as the original path; in the Opposite condition, they were asked to take the parallel path in the opposite direction (see Fig. 1b). The Same condition required the same turn magnitude as the outbound path: for an initial 30° right turn, a parallel path in the same direction required turning 30° to the left as the response. In contrast, the Opposite condition required participants to turn through the supplementary angle: for an initial 30° right turn, a parallel path in the opposite direction required a response of turning 150° to the right. The long initial hallway provides exposure to the initial facing direction as a reference for turning parallel/antiparallel to that direction; it should have no impact on the response angle, because the magnitude of the turn is the primary information for this task.

The experimental design thus consisted of five initial angles (30°, 60°, 90°, 120°, 150°) × 2 initial turn directions (left, right) × 2 parallel tasks (Same, Opposite). There were six trials in each condition, with 60 trials per session, for a total of 120 trials. The two tasks were presented in separate sessions, in a counterbalanced order. Trials alternated between right and left initial turns, but were otherwise presented in a randomized order.

Analysis and predictions

The two tasks were crafted to probe potential execution errors in turning. If execution error increases as the turn angle increases, participants should show a greater error for large response angles than for small response angles, even if they encoded the outbound turn angle accurately (Fig. 2). These factors are confounded in the Same condition and traditional angle reproduction tasks in general, because the response angle *increases* with the encoding angle. In contrast, in the Opposite condition, the response angle *decreases* with the encoding angle, and thus execution error can be decoupled from the encoding angle. Thus, final orientation error directly tests the encoding-error model of path integration: if encoding error is the only source of systematic error, then the participant's final orientation in the two conditions will be equal and opposite for a given encoding angle (Fig. 2b). If orientation is not equal and opposite, then other sources of error could contribute to path integration (Fig. 2c).

As an example, suppose a person makes an initial 30° turn, but encodes it as 45°. Then, they should respond by turning 45° (an overturn of 15°) in the Same condition, and

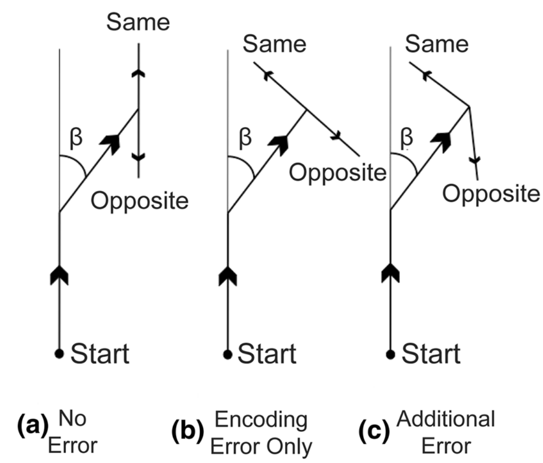

Fig. 2 Possible patterns of results. **a** Pattern of results given completely accurate performance, with no error from any source. Same and Opposite are 180° apart, both parallel to the original line. **b** Possible pattern of results if encoding error is the only source of systematic error. Same and Opposite are 180° apart, but not parallel to the original line. **c** Possible pattern of results if additional execution error is involved

turning 135° (an underturn of 15°) in the Opposite condition (see Fig. 2b). That is, the responses to the same initial turn angle should be 180° apart. In contrast, responses that differ significantly from 180° apart would imply a contribution of execution error (e.g., Fig. 2c). Because we tested for differences of 180°, we normalized the errors by subtracting 180° from the Opposite condition and then compared the errors directly.

Analysis was conducted in Matlab (Mathworks). Right and left initial turns were not significantly different and so were collapsed. The first analysis was performed on the normalized final orientation error. All trials were normalized to right-handed outbound rotations, with negative orientation error indicating a final orientation to the left of parallel (parallel is 0) and positive values indicating an orientation to the right of parallel. Because the null hypothesis is that encoding error is the only source of systematic error (i.e., there is no execution error), we tested whether the orientation error in the Same and Opposite conditions were 180° apart. To realize this test, the Opposite condition was normalized by subtracting 180°, and the orientations in the two conditions were then directly compared using a one-way Watson–Williams test (Batschelet 1981). The orientation error for each initial encoding angle in the Same condition was compared to the normalized orientation error for the same initial encoding angle in the Opposite condition, yielding five comparisons. If this comparison is significant, the difference may be attributed to execution error.

A second analysis was performed on signed angular error, the difference between the ideal orientation, and the actual orientation of the participant at the end of the trial.

Positive error indicates an overshoot in the turn response, while a negative error indicates an undershoot. To eliminate any effect of execution error, trial types were re-sorted, so that the required response angle in the Same and Opposite conditions was equated. For example, the errors in the Same condition with a 30° encoding angle were compared with the errors from the Opposite condition with a 150° encoding angle; both require a turn response of 30°, so any execution error would be equal in the two conditions. Thus, any significant difference between the Same and Opposite conditions may be attributed to encoding error. Finally, within-subject angular deviations (AD, the circular equivalent of the standard deviation) provided a measure of the variability, and hence the precision of each participant's responses. Signed angle errors and the angular deviations were analyzed using Watson–Williams one-way tests (Batschelet 1981). Currently, there are no higher order ANOVAs available for circular data, so pairwise comparisons between means were tested as separate Bonferroni-corrected one-way effects.

For both the orientation and signed angular errors, an additional analysis was performed on linearized angular values (between −180° and +180°) with repeated measures ANOVAs, to take advantage of the within-subject design of the experiment. Some of our comparisons predicted no difference between conditions, so we also computed Bayes factors for these two measures using the BayesFactor package in R. A Bayes factor indicates how much more strongly a model under consideration is supported than an alternative, often the null. Because we used a within-subjects design, we report comparisons between the experimental factors plus subject factors and a subject-only model.

Results

Final orientation error

Mean normalized final orientation error is plotted as a function of initial encoding angle in Fig. 3a. The final orientation in the Opposite condition was normalized by subtracting 180° from all values to directly compare it with the final orientation in the Same condition. Thus, the normalized orientations should be equal if encoding error is the only source of systematic error, and different if there is significant execution error. After Bonferroni correction for multiple tests (corrected *p*-threshold 0.025), all but one of the one-way Watson–Williams comparisons were significantly different, indicating that the final orientations in the Same and Opposite conditions were not 180° apart for four of the five initial turn angles (30° encoding angle: $F_{1,12} = 5.157$, $p = 0.042$; 60°: $F_{1,12} = 6.988$, $p = 0.021$; 90°: $F_{1,12} = 10.946$, $p = 0.006$; 120°: $F_{1,12} = 11.386$, $p = 0.006$; 150°: $F_{1,12} = 10.537$, 0.007). The mean difference between conditions was 33.46°. This result is consistent with a significant contribution of execution error.

We further examined this question by performing a more sensitive two-way analysis to test both main effects and their interaction. To do so, we normalized orientation error on a linear scale (between −180° and +180°), and applied a two-way repeated measures ANOVA (5 encoding angles × 2 conditions). We found a main effect of encoding angle ($F_{4,48} = 36.789$, $p < 0.001$, $\eta_p^2 = 0.754$), a main effect of Same/Opposite condition ($F_{1,12} = 8.242$, $p = 0.014$, $\eta_p^2 = 0.407$), and a significant angle × condition interaction

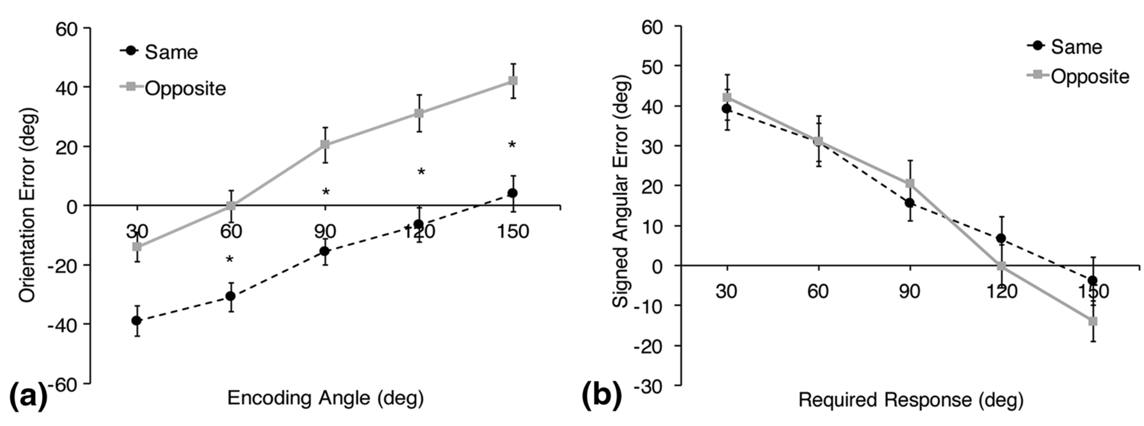

Fig. 3 **a** Test for execution error: final orientation error as a function of initial encoding angle. If there were no systematic execution error, there should be no difference between normalized orientation in the Same and Opposite conditions. *Different with $p < 0.05$ (Bonferroni corrected). A two-way ANOVA found a significant main effect of condition, suggesting a contribution of execution error, as well as a main effect of encoding angle and a significant interaction. **b** Test for encoding error: Signed errors as a function of required response angle. If there were no systematic encoding error, there should be no difference between errors in the Same and Opposite conditions. None of the comparisons were significantly different, suggesting a minimal contribution of encoding error. A two-way ANOVA found a significant main effect of response angle and a significant response angle × condition interaction, but no main effect of condition

($F_{4,48}=3.705$, $p=0.010$, $\eta_p^2=0.236$). The effect of condition is consistent with a significant contribution of execution error, while the main effect of encoding angle and interaction also suggests a contribution of encoding error. Examination of Bayes factors revealed that the condition + subject model was stronger than the subject-only model by a factor of 2.16×10^6 (±1.22%). The Bayes factor for the encoding angle + subject model was 1.53×10^5 (±0.42%). The strongest model was the condition + encoding angle + subject model, with a Bayes factor of 2.47×10^{14} (±1.92%) compared to the subject-only model.

Signed angular errors

The signed angular errors are plotted as a function of the required response in Fig. 3b, where the required response angle is matched in the Same and Opposite conditions (Fig. 3b). The signed error in the two conditions should be equal if execution error is the only source of error, and differ if there is significant encoding error. None of the paired Watson–Williams tests showed a significant difference between the Same and Opposite conditions, even without the Bonferroni correction for multiple comparisons (corrected p threshold 0.025) (30° response angle: $F_{1,12}=1.010$, $p=0.335$; 60°: $F_{1,12}=0.426$, $p=0.526$; 90°: $F_{1,12}=0.209$, $p=0.656$; 120°: $F_{1,12}=0.000$, $p=0.984$; 150°: $F_{1,12}=0.078$, $p=0.785$). This result implies that when matched for required response angle, the same pattern of errors is observed in the Same and Opposite conditions, regardless of the initial turn angle. For example, whether the initial angle is 30° or 150°, if the required response is to turn 30°, participants tend to overturn by the same amount in the two conditions. This result reveals no influence of encoding error, consistent with the primary source of error being execution error.

Signed errors were also analyzed using linearized angular values (−180° to +180°). A two-way ANOVA (5 required response angles × 2 conditions) found a main effect of response angle ($F_{4,48}=34.310$, $p<0.001$, $\eta_p^2=0.741$) and a response angle × condition interaction ($F_{4,48}=6.395$, $p<0.001$, $\eta_p^2=0.348$), but no effect of condition ($F_{1,12}=0.001$, $p=0.972$, $\eta_p^2=0.000$). These results suggest that the task of going in the Same or Opposite direction had little effect on angular errors (although the Same condition had a somewhat shallower slope, as evidenced by the significant interaction). In contrast, the required response angle demonstrated a strong effect, with overturns for small responses and underturns for large responses. Bayesian analysis of signed angular errors found a Bayes factor of 7.52×10^{13} (±1.3%) for response angle + subject over the subject-only model, whereas the condition + subject model had a factor of only 0.18 (±0.91%) over the subject-only model.

Angular deviation

Mean angular deviations in the Same and Opposite conditions were not significantly different.

Discussion

This experiment dissociated encoding and execution errors by requiring different responses to the same initial stimuli. The results indicate a substantial contribution of execution error in rotational path integration. First, when analyzed by initial turn angle, final orientation error in the Same and Opposite conditions was significantly different. That is, when asked to walk parallel to their initial path, responses in the same direction were not 180° from responses in the opposite direction, but were off by an average of 33°. For example, when reproducing an initial 60° angle, participants made greater errors in the Same condition (requiring a 60° turn) than in the Opposite condition (requiring a 120° turn). This demonstrates a significant level of execution error in angle reproduction.

In contrast, when analyzed by the required response angle, the signed errors were highly similar in the Same and Opposite conditions, with no significant differences. For example, when the correct response was a 60° turn, participants made equivalent errors when reproducing a 60° angle in the Same condition and a 120° angle in the Opposite condition (overturing by 30° in both). The data were consistent with an execution error that was proportional to the response angle, but offered no evidence of an encoding error that depended on initial angle. However, we found a main effect of encoding angle in the orientation errors, indicating that encoding could contribute to some systematic error. Yet, there was also a main effect of condition, suggesting that encoding errors are not the full story. When paired only by the response angle, which have different encoding angles, there were no differences between conditions in signed angular error, suggesting that execution error is the primary source of systematic error.

A possible concern about the experimental method is that we compared two slightly different tasks: walking parallel to the original path in the Same (original) direction, or in the Opposite (180° from the original) direction. It is possible that the Opposite condition required an additional operation before executing a response, such as mentally rotating an allocentric reference frame by 180° or computing the supplementary angle, which could have contributed to the observed differences in final orientation between the two conditions (Fig. 3a). However, when the response angle was equated, this difference was eliminated (Fig. 3b), implying that any such mental operation in the Opposite condition did not contribute to rotation error. Nevertheless, we control for this possibility in the design of Experiment 2.

Taken together, these results indicate significant execution errors that overshoot small turns and undershoot large turns, but little encoding error. This pattern of overshoots and undershoots agrees qualitatively with previous angle reproduction experiments (e.g., Israel et al. 1996; Jürgens et al. 2003; Klatzky et al. 1990; Loomis et al. 1993).

Experiment 2

Experiment 1 established that execution error plays a major role in angular path integration, while the role of encoding error was unsupported. However, the method left two unresolved issues. First, the analyses compared slightly different tasks in the Same and Opposite conditions. Second, Experiment 1 tested a limited range of response angles (30°–150°), and the findings need to be generalized over a wider range. Experiment 2 addresses both of these concerns by asking participants to respond by turning in either the "short" or the "long" direction to walk parallel to their original path in the Same and Opposite conditions. This allows us to compare different response angles with the same task.

Methods

Participants

Fifteen female and ten male volunteers were paid for their participation. Ages ranged from 19 to 56 (mean 24.06). Four participants were excluded from analysis due to technical errors and one was excluded for not following instructions, yielding twelve female and eight male participants completing the study. All participants were informed of the potential risks of the study and signed to indicate their informed consent in fulfillment of the requirements of the Brown University IRB.

Equipment

The apparatus was the same as in Experiment 1, except that the virtual environment was generated on a Dell graphics PC and presented in a Rockwell–Collins SR80A HMD (63° H × 53° V field of view, 1280 × 1024 pixels, 60 Hz frame rate). Participants wore a backpack containing the control box for the HMD, a power supply, and some additional cables, which weighed approximately eight pounds and did not impede movement.

Procedure

The procedure was the same as in Experiment 1, with the following exceptions. The response types (Parallel Same and Opposite) were demonstrated using tape on the floor at a reduced scale. Participants were asked to make several practice responses to confirm that they understood the instructions. Experimental trials were blocked by response type over three experimental sessions, with four blocks per session (one block each of Parallel Same and Parallel Opposite, and two blocks of tasks not reported here), with frequent opportunity for breaks. Instructions were presented over headphones at the beginning of each block for the response type (e.g., Parallel Same) and were repeated on each trial (e.g., "turn right to go parallel in the same direction"). The experimental component of each session lasted 40–60 min.

Tasks

The virtual environment was the same as in Experiment 1, except that the hallway was 1.5 m wide, the cylindrical hedge had a 1.5 m radius, and there were six initial turn angles (30°, 60°, 90°, 120°, 150°, and 180°).

The two parallel response types (Same or Opposite) were the same as before. In addition, verbal cues presented over headphones directed participants to respond by turning right or left onto these parallel paths. Thus, participants made both short and long turns to reach the response orientation. For example, for a 30° initial turn, the "short" way to turn and face the parallel Same direction was to turn 30°, whereas the "long" way was to turn 330° (Fig. 1c).

The experimental design consisted of 6 initial turn angles (30°, 60°, 90°, 120°, 150°, 180°) × 2 initial turn directions (left, right) × 2 parallel tasks (Same, Opposite) × 2 response turn directions (short, long). There were two trials in each condition, for a total of 96 trials. Trials were presented in blocks by task, with 14 trials per block on day 1 and 17 trials per block on days 2–3. Blocks were presented in a random order with the constraint that a block with each response type was presented once per session.

Analysis and predictions

The dependent measures were the same as in Experiment 1. In Experiment 2, the final orientation error and signed angular error for the Same and Opposite conditions were analyzed separately, by comparing the "short" and "long" turning directions within a given condition. An additional analysis was performed on linearized angular values (between −180° and +180°) with repeated measures ANOVAs, to take advantage of the within-subject design of the experiment.

This design allows us to compare different required response angles while holding the initial encoding angle and the task constant. If encoding error is the only systematic component of rotational error, then the final orientation should be the same for both the "short" and "long" turn direction. In contrast, if execution error contributes to rotational errors, then the final orientations for the "short" and "long" turns will differ. As in Experiment 1, if execution error dominates, then trials that have the same required response angle, but different encoding angles, should exhibit similar errors.

For reasons, we will outline in more detail below, and we analyzed the 180° encoding angle for both the Same and Opposite conditions separately from the other conditions. Briefly, it was unclear in these conditions whether the responses at this encoding angle reflected encoding errors or execution errors.

Results

Final orientation error

Mean final orientation error at each initial encoding angle appears in Fig. 4a for the Same condition, and in Fig. 4b for the Opposite condition. If encoding error is the only source of error, then the "short" and "long" responses should be comparable, whereas if execution error contributes they should differ. Watson–Williams tests compared the matched "short" and "long" responses at each encoding angle. In the Same condition (Fig. 4a), two of the five comparisons showed marginally significant differences after Bonferroni correction, although the rest were not significantly different (30° encoding angle: $F_{1,19}=0.304$, $p=0.588$; 60°: $F_{1,19}=1.405$, $p=0.251$; 90°: $F_{1,19}=5.527$, $p=0.030$; 120°: $F_{1,19}=3.177$, $p=0.091$; 150°: $F_{1,19}=5.882$, $p=0.025$). In the Opposite condition (Fig. 4b), four out of the five comparisons were significantly different and one marginally significant, after Bonferroni correction (30° encoding angle: $F_{1,19}=16.293$, $p<0.001$; 60°: $F_{1,19}=13.116$, $p=0.002$; 90°: $F_{1,19}=12.250$, $p=0.002$; 120°: $F_{1,19}=7.668$, $p=0.012$; 150°: $F_{1,19}=5.737$, $p=0.027$). These findings suggest that execution error may contribute to overall rotational error.

We pursued this question by performing a more sensitive two-way analysis to test both main effects and their interaction. To do so, we normalized orientation error on a linear scale (between −180° and +180°), and applied a two-way repeated measures ANOVA (5 encoding angles × 2 response turn directions). Once again, if encoding error is the only source of systematic error, then "short" and "long" responses should be similar, but if there is significant execution error, they should differ. In the Same condition, there was a main effect of encoding angle ($F_{4,76}=13.718$, $p<0.001$, $\eta_p^2=0.419$), a main effect of response turn direction (short/long) ($F_{1,19}=8.544$, $p=0.009$, $\eta_p^2=0.310$), but no interaction ($F_{4,76}=1.748$, $p=0.148$, $\eta_p^2=0.084$). The Bayes factor for the encoding angle + subject model was 7674.82 (±0.66%), and was 4730.01 (±2.11%) for response turn direction + subject compared to the subject-only model. The strongest support was for the encoding angle + response turn direction + subject model, with a Bayes factor of 2.20×10^8 (±2.04%) compared to the

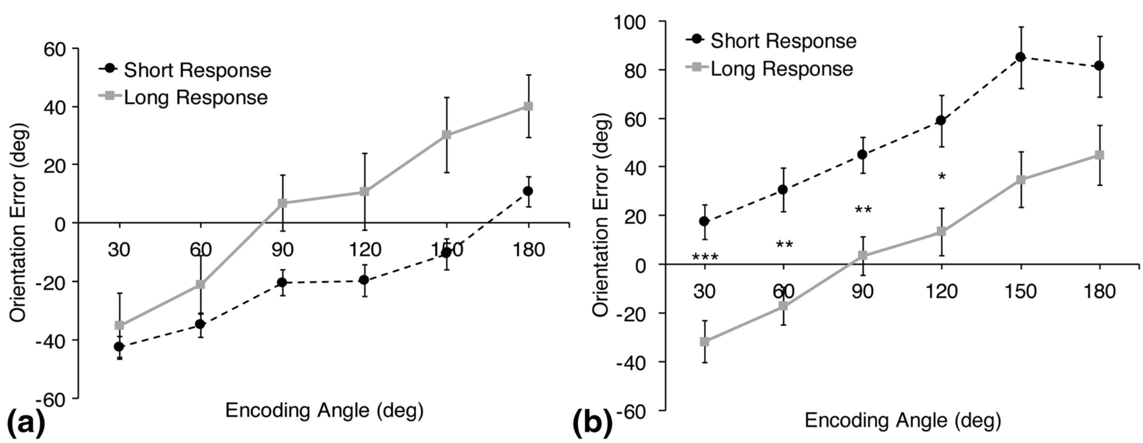

Fig. 4 Test for execution error: final orientation error as a function of initial encoding angle, for short and long response turn directions. If there were no systematic execution error, final orientation should be the same for both responses. **a** Same condition. **b** Opposite condition. *Different with $p<0.05$, **different with $p<0.01$, ***different with $p<0.001$ (Bonferroni corrected). Two-way ANOVAs found significant main effects of encoding angle and response direction, but no interaction for the Same condition (**a**), and significant main effects of encoding angle and response direction, as well as a significant interaction for the Opposite condition (**b**). These results are consistent with a significant contribution of execution error. The 180° encoding angles were not included in either analysis

subject-only model. In the Opposite condition, there was also a main effect of encoding angle ($F_{4,76} = 11.194$, $p < 0.001$, $\eta_p^2 = 0.371$), a main effect of turn direction ($F_{1,19} = 4.747$, $p = 0.042$, $\eta_p^2 = 0.200$), and a significant interaction ($F_{4,76} = 3.161$, $p = 0.019$, $\eta_p^2 = 0.143$), indicating that the difference between short and long responses depends on encoding angle. The Bayes factor for encoding angle in the Opposite condition was 627.14 (±0.38%) and was 4472.11 (±0.78%) for response turn direction compared to the subject-only model. The strongest support was for the encoding angle + response turn direction + subject model, with a Bayes factor of 1.14×10^7 (±0.93%). These results are consistent with a significant contribution of execution error.

Signed angular errors

Signed angular errors as a function of the required response angle appear in Fig. 5, where the response angle is matched in the Same and Opposite conditions. If systematic rotational errors are due solely to execution error, then the error in the two conditions should be comparable, because the required response is equated; in contrast, if encoding error makes a significant contribution, then they should differ, because the initial encoding angles do. Watson–Williams tests comparing the Same and Opposite conditions at each required response angle revealed that only two out of ten possible contrasts were significantly different, even without the Bonferroni correction (30° response angle: $F_{1,19} = 7.651$, $p = 0.012$; 60°: $F_{1,19} = 3.615$, $p = 0.073$; 90°: $F_{1,19} = 7.081$, $p = 0.015$; 120°: $F_{1,19} = 0.906$, $p = 0.353$; 150°: $F_{1,19} = 0.517$, $p = 0.481$; 210°: $F_{1,19} = 0.009$, $p = 0.925$; 240°: $F_{1,19} = 0.130$, $p = 0.723$; 270°: $F_{1,19} = 0.557$, $p = 0.465$; 300°: $F_{1,19} = 0.247$, $p = 0.625$; 330°: $F_{1,19} = 0.001$, $p = 0.980$). The 180° and 360° response angles were analyzed separately below. Altogether, these results suggest that encoding error may play a role in some cases, but it is not a major contributor to overall rotational error.

Signed errors were also analyzed using linearized angular values (−180° to +180°). A two-way ANOVA (10 required response angles × 2 task conditions) found only a main effect of required response angle ($F_{9,171} = 15.395$, $p < 0.001$, $\eta_p^2 = 0.448$), with no effect of condition ($F_{1,19} = 0.304$, $p = 0.588$, $\eta_p^2 = 0.016$) or interaction ($F_{9,171} = 0.816$, $p = 0.602$, $\eta_p^2 = 0.041$). This result is consistent with a minimal contribution of encoding error. In support of these findings, the Bayes factor for the condition + subject model was only 0.13 (±2.06%) over the subject-only model. In contrast, the model with the strongest support was the response angle + subject model, with a Bayes factor of 4.18×10^{18} (±0.37%) over the subject-only model.

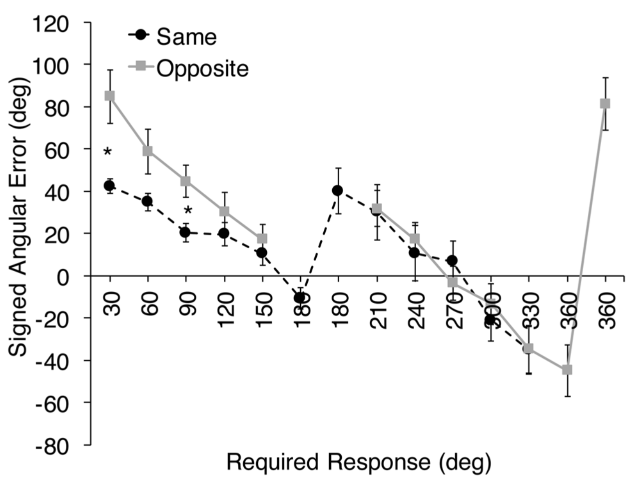

Fig. 5 Test for encoding error: signed error as a function of required response angle. If there were no systematic encoding error, then there should be no differences between the Same and Opposite conditions. *Different with $p < 0.05$ (Bonferroni corrected). A two-way ANOVA found a significant main effect of required response angle. These findings are consistent with a minimal contribution of encoding error. Both the 180° required responses came from the Same condition and both the 360° required responses came from the Opposite condition, and so two entries for those responses are reported, but were not included in the analysis

180° encoding angle

In the Same condition, the 180° encoding angle requires a 180° response in both the so-called "short" and "long" turn directions (Fig. 4a). Likewise, in the Opposite condition, the 180° encoding angle requires a 360° turn in both the "short" and "long" directions (Fig. 4b). Significant differences between the "short" and "long" responses in these cases could signify a contribution of encoding error, because the required responses are the same. However, the encoding angles are also the same, making it difficult to determine whether differences between these conditions are due to encoding or execution error. The Watson–Williams tests comparing the 180° encoding angle in the Same condition found a marginal difference after Bonferroni correction (180°: $F_{1,19} = 4.865$, $p = 0.040$), whereas in the Opposite condition, there was no difference between the "short" and "long" directions (180°: $F_{1,19} = 2.797$, $p = 0.111$).

Angular deviations

The mean within-subject angular deviations (AD) at each encoding angle appear in Fig. 6a. Significant differences in

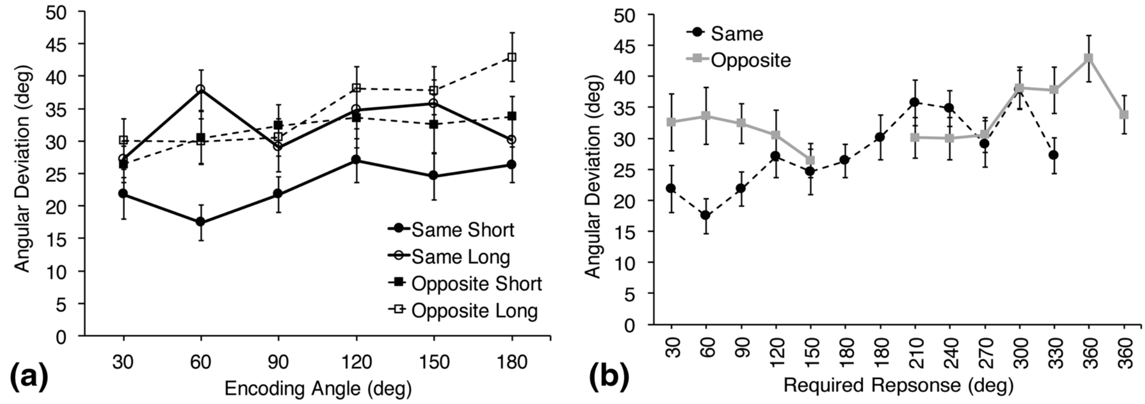

Fig. 6 **a** Within-subject angular deviations, arranged by encoding angle. There was a significant main effect of response length (short vs long) for the Same condition, whereas for the Opposite condition, there were no significant effects. The low angular deviations in the same short condition are consistent with an intrinsic (action-scaled) metric for rotation. **b** Within-subject angular deviations, arranged by required response angle. There was a significant main effect of required response, condition, and a significant interaction. Both the 180° required responses came from the Same condition and both the 360° required responses came from the Opposite condition, and so two entries for those responses are reported, but were not included in the analysis

AD at the same encoding angle would be due to variable error in execution, given that encoding error is equated. A two-way repeated-measures ANOVA (5 encoding angles × 2 response turn directions) for the Same condition revealed no main effect of encoding angle ($F_{4,76} = 1.573$, $p = 0.190$, $\eta_p^2 = 0.076$), a significant difference between "short" and "long" response turns ($F_{1,19} = 14.787$, $p = 0.001$, $\eta_p^2 = 0.438$) and no interaction ($F_{4,76} = 1.942$, $p = 0.112$, $\eta_p^2 = 0.093$). Responses in the "short" direction had much lower variability than those in the "long" direction. For the Opposite condition, there was no main effect of encoding angle ($F_{4,76} = 1780$, $p = 0.142$, $\eta_p^2 = 0.086$), no effect of response turn direction ($F_{1,19} = 0.762$, $p = 0.394$, $\eta_p^2 = 0.039$), and no interaction ($F_{4,76} = 0.588$, $p = 0.672$, $\eta_p^2 = 0.030$). Finally, when sorting the ADs by required response angle (replotted in Fig. 6b), a two-way ANOVA revealed a main effect of the required response ($F_{9,171} = 3.083$, $p = 0.002$, $\eta_p^2 = 0.140$), as well as a main effect of Same/Opposite condition ($F_{1,19} = 6.199$, $p = 0.022$, $\eta_p^2 = 0.246$), and a significant interaction ($F_{9,171} = 2.368$, $p = 0.015$, $\eta_p^2 = 0.111$). These results suggest that variable error in execution increases as the response angle increases and that "short" response turns in the Same condition have the lowest variability overall.

Discussion

The results of Experiment 2 confirm a contribution of execution error to rotational path integration, as observed in Experiment 1. In addition, the contribution of encoding error appears minimal. In contrast to Experiment 1, we also found differences in within-subject angular deviations, due largely to greater variability in executing longer response turns.

First, consider the hypothesis that execution error contributes a significant component to overall systematic rotational error. When final orientation error is plotted by encoding angle, thereby equating encoding error (Fig. 4), four out of the ten comparisons between "short" and the "long" turns were significant, and another three marginally so. These results demonstrate a role of execution error, although they are not as strong as in Experiment 1. However, the two-way analysis found a significant effect of short/long turn and interactions with encoding angle, supporting substantial execution error.

Second, consider the hypothesis that encoding error is a significant contributor to systematic rotational error. When the data are sorted by the required response angle, thereby equating execution error, there is little difference in signed error between the Same and Opposite conditions, which have different encoding angles (Fig. 5): only two out of the ten comparisons were significant and there was no Same/Opposite main effect in the two-way analysis, but there was a main effect of required response angle. These findings imply a minimal contribution of encoding error and instead suggest a primary role for execution error. There are two subtleties in the pattern of results, however.

One is that final orientation error increases with encoding angle (Fig. 4). This effect was significant in both the Same and Opposite conditions, and can be seen in both "short" and "long" responses. This observation suggests a contribution of encoding error, but execution error can also largely explain the results in this experiment. As Fig. 5 illustrates, when the data are sorted by the required response angle, there is a larger main effect in which participants overturn small-to-medium required angles and underturn large required angles. This observation is consistent with angle and distance reproduction tasks in the human path integration literature (e.g., Bakker et al. 1999; Jurgens et al. 2003). That said, encoding error likely plays some role in these reproduction errors.

The other is the exceptional results with an encoding angle of 180°. The mixed finding suggests that there may be a small contribution of encoding error for 180° turns. In particular, the participant may be confused as to whether they had crossed the 180° axis during encoding. In addition, the marginal difference in the Same condition could be related to the difference between "unturning" and the mental computation of completing a rotation based on an external metric; the lower errors in the "short" condition could be evidence for an intrinsic metric. The difference in errors between the Same and Opposite condition could also reflect the mental operation of making an Opposite response.

The analysis of within-subject angular deviations revealed that the lowest variable error occurs with "short" responses in the Same condition. These trials are the closest to pure angle reproduction. Thus, in their response, participants could simply be matching (or canceling) the idiothetic information from their initial turn, consistent with an intrinsic metric for rotation. In addition, there is modest support for the hypothesis that larger response angles lead to greater angular deviations, especially in the case of Same "long" and Opposite "long" trials, due to variable error in execution.

General discussion

These two experiments examine the contribution of sources of rotational error in path integration and provide the groundwork for determining whether angular integration uses an intrinsic or extrinsic metric. Specifically, we dissociated systematic encoding errors and execution errors in an angle reproduction task. Experiment 1 revealed that execution error makes a significant contribution to rotational error. When the data were plotted by encoding angle, thereby equating encoding errors, final orientation differed between Same and Opposite response conditions, consistent with significant execution error. In contrast, when the data were sorted by the required response angle, thereby equating execution errors, there were no differences between the two conditions, thus providing no evidence of encoding error. Experiment 2 controlled for these slightly different task conditions by comparing "short" and "long" turns within the same task, and expanded the range of response angles. The results confirmed substantial execution error, including both constant and variable errors, but observed only marginal encoding error.

The present experiments found little evidence for systematic encoding error in rotational path integration. In Experiment 1, conditions with the same encoding angles produced different patterns of errors, whereas conditions with different encoding angles yielded comparable patterns of errors. In Experiment 2, the pattern of results was similar, except for two conditions in which different encoding angles did produce significantly different errors. Encoding error thus made a minimal contribution to overall rotational error. These findings stand in contrast to previous reports that have presented angle reproduction data as indicators of pure encoding error (e.g., Sadalla and Montello 1989) or have assumed that all systematic errors stem from encoding error alone (e.g., Fujita et al. 1993).

On the other hand, the present results provide the first evidence for execution error in rotational path integration. In Experiment 1, conditions with different required response angles produced different patterns of errors, whereas conditions with matched required responses yielded comparable errors. The pattern of results was similar in Experiment 2, except for a few errant conditions. Bakker and colleagues (1999, 2001) previously reported execution errors when participants produced verbally-specified angles that were aligned with cardinal reference axes. The present experiments demonstrate large execution errors in angle reproduction when responses matched rotations made in the initial phase of a trial. Current models of path integration do not incorporate execution error (Benhamou and Seguinot 1995; Fujita et al. 1993). An important implication of our findings is that execution error must be incorporated into future models.

We wish to note that "execution error" may actually include some element of encoding error (see Chrastil and Warren 2014). It is unlikely that the execution of a response is ballistic (execution of a preset motor plan); more likely, the navigator monitors (encodes) the magnitude of rotation during the response until the intended turn is complete. So far, attempts to separate out the contribution of this form of encoding error from pure execution error during the response have been unsuccessful. One likely possibility is that the encoding error during the rotation and the response is equal; in that case, the encoding errors would cancel, and the reproduction error would reflect residual execution error. Under this model, our finding of significant errors in simple reproduction (Fig. 3a "Same" and Fig. 4a "Short") suggests that there are significant execution errors. In the scenario that the encoding errors differ between rotation and response, what is referred to as "execution error" probably includes elements of both encoding and execution error.

The present results also provide moderate support for the hypothesis that rotational path integration has an intrinsic (action-scaled) rather than an extrinsic (objective) metric. One the one hand, participants in Experiment 1 reported a preference for the Same task condition, saying that they attempted to “unturn” the initial encoding angle. This result suggests that they tried to match (or cancel) the intrinsic idiothetic information encoded on the initial turn, whereas using extrinsic information would likely have resulted in an equally challenging task for all conditions. Israël and Warren (2005) reported that, when given a choice, participants prefer to “unturn” angles rather than complete the circle, and these inversions are less variable than the completions. In a related study, Arthur et al. (2012) found that using egocentric response modes reduced the effects of spatial context in angle estimation compared to using allocentric response modes, suggesting greater stability when using intrinsic metrics. Similarly, in our Experiment 2, within-subject variability was lowest in the “short” Same condition, which corresponds to “unturning” or inverting the angle.

Some researchers have reported that participants preferably encode the outbound velocity profile and reproduce it during the response (Berthoz et al. 1995; Glasauer et al. 2007; Israel and Berthoz 1989; Israel et al. 1997; Israël and Warren 2005; Ivanenko et al. 1997). This could be one form of an intrinsic metric. Glasauer et al. (2007) found that the reproduced velocity profile accounted for approximately 70% of the variance in a rotation task. Others have found no evidence for velocity matching, however (Israel et al. 1996; Siegler et al. 2000; Vidal and Bülthoff 2010). Preferences for both “unturning” and matching velocity profiles are consistent with an intrinsic metric.

On the other hand, participants performed the Same and Opposite tasks with comparable accuracy, even though the Same task allows for the use of intrinsic information by “unturning”, whereas the Opposite task favors the use of an extrinsic metric by requiring a turn through the supplementary angle. Constant error was related to the required response angle, not the encoded angle, suggesting that participants did not match information on the initial and final turns, consistent with an extrinsic metric. Note that these experiments required participants to keep track of several different tasks. For example, participants in Experiment 2 were not instructed to turn in the “short” or “long” direction until after they made the initial turn and were ready to respond. Participants may have coped with these task demands by relying on a more flexible extrinsic metric. Recall, however, that variable error was lowest in the “short” Same condition, indicating that “unturning” was most precise, consistent with the intrinsic hypothesis. In sum, our results suggest that both intrinsic and extrinsic metrics could be used during path integration, but that intrinsic metrics are likely preferred and tend to be more accurate and/or precise.

Conclusions

We examined the contribution of systematic encoding and execution errors in angular path integration by dissociating the required response angle from the encoding angle. We found that participants overturned small angles and underturned large angles and that errors were related to the required response angle, not the encoding angle. Even when controlling for the task (Same/Opposite), errors depend on the magnitude of the response rather than the magnitude of the encoding angle. These findings suggest that execution error makes the largest contribution to rotational errors in path integration, whereas encoding error contributes minimally. Our findings also offer some support for an intrinsic metric in angular path integration, although the evidence is stronger in linear path integration (Chrastil and Warren 2014).

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