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# Vision and proprioception make equal contributions to path integration in a novel homing task

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ABSTRACT

Navigation is a vital cognitive function for animals to find resources and avoid danger, and navigational processes are theorized to be a critical evolutionary foundation of episodic memory. *Path integration*, the continuous updating of position and orientation during self-motion, is a major contributor to spatial navigation. However, the most common paradigm for testing path integration—triangle completion—includes potential sources of error that cannot be disentangled. Here, we introduce a novel loop closure paradigm to test path integration, including the relative contributions of visual and body-based cues to performance. Contrary to triangle completion, we found that vestibular information alone led to chance performance, while visual optic flow and proprioception made relatively equal and independent contributions. The integration of these two cues was previously unknown, and we found that the two cues were not integrated in a Bayesian ideal manner. Our novel paradigm demonstrates the importance of both vision and proprioception to human path integration and provides the first test of optic flow and proprioception Bayesian cue combination for homing behavior. These findings open up new avenues to study navigation.

1. Introduction

In order to successfully navigate in complex environments, animals rely on multiple navigation processes, such as landmark-based systems or path integration. *Path integration* is the constant updating of position and orientation during self-motion (Mittelstaedt & Mittelstaedt, 1982, 1980). Path integration is important for navigating in environments without landmarks, such as deserts or the open ocean, but also for learning metric information about distances and angles in more complex environments. It is theorized to be the underlying mechanism for the acquisition of map-like survey knowledge (Gallistel, 1990; Wang, 2016) and could facilitate learning local metric information to support other types of spatial knowledge, such as labeled graphs (Chrastil & Warren, 2014b). Researchers have also suggested that path integration is an evolutionary source for episodic memory (Burgess, Maguire, & O'Keefe, 2002; Hasselmo, 2009).

Despite our reliance this navigational skill, we do not fully understand the contributions of visual and body-based (or *idiothetic*) information to path integration. Furthermore, the most common paradigm for testing path integration—triangle completion—introduces potential sources of error that cannot be disentangled. In addition, it has not yet been determined whether or how optic flow and proprioceptive cues are integrated during homing. Here, we introduce a novel paradigm to test path integration, which we used to investigate the relative contributions of visual and idiothetic information.

1.1. Sources of error during path integration

Current methods of studying path integration have relied upon the *triangle completion task* (Kearns, Warren, Duchon, & Tarr, 2002; Klatzky, Loomis, Beall, Chance, & Golledge, 1998; Loomis et al., 1993; Tcheang, Bülthoff, & Burgess, 2011). In this task, a participant is guided on two legs of a triangle, then must turn and walk back to the home location, where they began. This homeward trajectory allows participants to move in a free and naturalistic way, but makes it difficult to pinpoint the source of systematic errors during path integration. These errors could stem from (1) *Encoding* the distances and angles of the outbound path, (2) *Integrating* the trajectory of the homeward path, and (3) *Executing* the homebound trajectory (Fujita, Klatzky, Loomis, & Golledge, 1993; Loomis et al., 1993). The relative contribution of execution error is currently undetermined, and some researchers propose that it makes minimal contribution (Fujita et al., 1993; Klatzky, Beall, Loomis, Golledge, & Philbeck, 1999; Loomis et al., 1993). The relatively accurate performance in blind walking to targets (Loomis, da Silva, Fujita, & Fukusima, 1992; Thomson, 1983) has been used to justify this assumption of no systematic error from execution error.

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Despite these assumptions, the unique contributions of execution error cannot be fully mathematically disentangled from encoding error in standard distance or angle reproduction tasks (Chrastil & Warren, 2014a). Furthermore, our previous research has found substantial execution error even in simple tasks (Chrastil & Warren, 2017). In that experiment, we asked participants to make differing production responses to the same outbound rotational stimuli, thereby controlling for potential encoding errors. We found evidence for substantial execution errors when the encoding angle was held constant while the execution angle varied. Those findings indicate that the assumption that encoding is the source of most error in triangle completion—and by extension path integration in general—does not hold. To circumvent the potential confounds of execution error, we created a task that does not require the production of a homebound trajectory: loop closure.

1.2. Loop closure

The loop closure task relies on the simple shape of a circle. Participants are guided by an experimenter in a circular trajectory while mentally tracking their start location, pressing a button when they think they have returned to the start location. This task allows us to precisely measure errors based on how well participants track the start, which could range from very far undershoots to very far overshoots. Furthermore, we can vary the radii of the loops to determine whether errors drift more with larger sizes or whether tracking remains invariant across scale. This task is related to the idea of loop closure in simultaneous localization and mapping (SLAM), a robotics navigation system. SLAM uses visual scene information to correct for errors accumulated during self-motion (Durrant-Whyte & Bailey, 2006); our task deals with accumulated errors without the visual scene corrections.

We previously introduced a variant of a loop task as part of an fMRI study (Chrastil, Sherrill, Hasselmo, & Stern, 2015). In that study, we showed participants videos of circular movement and asked whether the video returned to the starting place. We found that the hippocampus, retrosplenial cortex, and parahippocampal cortex tracked Euclidean distance from the start location, consistent with a *homing vector* model of path integration, in which the navigator continuously tracks their position relative to the home location without having to remember the path (Fujita, Loomis, Klatzky, & Golledge, 1990; Philbeck, Klatzky, Behrmann, Loomis, & Goodridge, 2001). In contrast, most computational and animal models of navigation in neuroscience rely on a *configural model*, in which the navigator tracks only the configuration of the path (Benhamou, Sauve, & Bovet, 1990; Fujita et al., 1993; Klatzky, Loomis, & Golledge, 1997; May & Klatzky, 2000; H. Mittelstaedt & Mittelstaedt, 1982). Evidence suggests that humans can use either strategy depending on the task (He & McNamara, 2017; Wiener, Berthoz, & Wolbers, 2011). Thus, the loop closure task has the promise to open new perspectives in both human neuroscience and computational models of navigation and memory.

In our previous study, however, we could not test for systematic errors because that version did not allow for the free report of the start location. Furthermore, we used purely visual stimuli in the fMRI scanner, so we were unable to test the extent to which vision contributes to this paradigm compared with body-based cues. Therefore, we developed the present task to test for systematic errors in path integration, including both accuracy and precision, under differing levels of sensory information.

1.3. Information from self-motion during path integration

The relative contributions of body-based information and visual optic flow information to path integration is not fully understood. Visual information from optic flow is sufficient for distance judgments and triangle completion; although systematic errors occur under conditions of vision only, performance is not random (Ellmore & McNaughton, 2004; Kearns et al., 2002; Riecke, 2002). Results have been more mixed on the contributions of vestibular or proprioceptive information. For example, some investigators have found large errors under conditions of visual input only or imagined walking, but reduced errors with physical walking and active rotations (Campos, Byrne, & Sun, 2010; Chance, Gaunet, Beall, & Loomis, 1998; Kearns et al., 2002; Klatzky et al., 1998). In contrast, other studies found that adding proprioception to vestibular or visual information yields little improvement (Allen, Kirasic, Rashotte, & Haun, 2004; Campos, Butler, & Bülthoff, 2012; Ehinger et al., 2014), or even found dominance of visual information (Koutakis, Mukherjee, Vallabhajosula, Blanke, & Stergiou, 2013). These findings suggest minimal proprioceptive contributions. However, most of these studies either examined only one cue type, did not add visual optic flow, or did not test a vestibular information only condition.

It is also important to consider whether navigators combine the information from these multiple cues in an optimal way, maximizing information. Bayesian cue combination analysis (Ernst & Banks, 2002; Landy, Maloney, Johnston, & Young, 1995) examines the within-subject variance under each cue separately as well as under a combined cue condition, which should ideally have a much lower variance. Although a few studies have examined cue combination in triangle completion, (Chen, McNamara, Kelly, & Wolbers, 2017; Nardini, Jones, Bedford, & Braddick, 2008; Zhao & Warren, 2015), the visual information in those studies came from landmarks, not optic flow self-motion cues. In a triangle completion study that used optic flow, Tcheang et al. (2011) found that visual and body-based information combine in some way to form a single model of self-motion. However, it is unknown whether these cues are optimally combined. Cue combination analysis of non-homing path integration tasks found that adults do not optimally integrate visual and body-based cues when reproducing a path (Petrini, Caradonna, Foster, Burgess, & Nardini, 2016), but the cues are optimally combined for estimating distance (Campos et al., 2010). Thus, whether optic flow and proprioception self-motion cues are combined in an ideal manner during homing remains unknown.

In sum, prior work has not fully orthogonalized vestibular, proprioceptive, and visual information. Furthermore, those studies used triangle completion tasks, which could confound and compound systematic errors during the production of the homebound path. Our loop closure paradigm circumvents these difficulties by eliminating the homebound production step. In addition, to our knowledge no study has examined cue integration of self-motion cues during homing behavior.

We tested our novel loop closure paradigm by fully examining both constant (mean) and variable (within-subject standard deviation) errors. Participants completed a baseline condition in a wheelchair without vision (vestibular only), in addition to three experimental conditions: wheelchair with vision (vestibular + vision), walking without vision (vestibular + proprioception), and walking with vision (vestibular + vision + proprioception). We also tested whether proprioception and visual cues are combined in an optimal Bayesian manner. Based on previous studies, we expected that proprioception would make a larger contribution than optic flow information to loop closure, but that the cues would be relatively optimally weighted.

2. Materials and methods

2.1. Participants

26 healthy young adults (11 female, 15 male) participated in this study. The sample size is based on previous path integration studies, with effect sizes in the 0.3–0.4 range. The design and all analyses were within-subjects, which helps control for between-subjects variance and allows for a moderate sample size. Three participants did not complete the study (1 female and 2 male) due to symptoms of simulator sickness and/or panic disorder in the virtual environment. Ages of the remaining 23 adults ranged from 18 to 22 (mean = 19.9, SD = 1.4), and all but

one were right-handed. All participants signed forms indicating their informed consent to be a part of the study, in accordance with a protocol approved by the University of California Santa Barbara Institutional Review Board. Participants received payment at the rate of $12 per hour for participating in the study.

2.2. Equipment, stimuli, and displays

The experiment was conducted in the UCSB Research Center for Virtual Environments and Behavior (ReCVEB), a 10 × 10-m ambulatory virtual reality facility. Images were presented to participants in an Oculus Rift stereoscopic head mounted display (HMD) (dual 680x480 pixel resolution, 50° horizontal × 38° vertical field of view, a 60 Hz refresh rate). Tracking of head position and orientation within ReCVEB was accomplished using a WorldViz 8-camera tracking system, with an update rate of 150 Hz. Total system latency was 65 ms. High resolution virtual environments were generated in Vizard 5 (WorldViz) and rendered using an NVIDIA GeForce GTX 970 dual pipe graphics card. Naturalistic evening noises were presented over headphones to interfere with any auditory location or orientation cues.

For vision conditions, participants saw a bare desert ground (textured ground plane) and a blue sky in a virtual environment (Fig. 1a). No landmarks or orienting cues were present. In order to simulate complete removal of visual input for the no-vision conditions, the displays in the HMD were of a black sky with the ground removed and the lights in the virtual world turned off. This setup gave our participants the effect of a completely black space.

For both vision and no-vision conditions, an orange triangular pole with red arrows (Fig. 1b) served as the start pole for each trial, which indicated the starting (home) location for each trial. The direction of the arrows indicated the direction the participants should face to start the trial. Participants were instructed to remember the start location as they moved along their path. We included the start pole to ensure that participants had explicit knowledge of the home location and the correct travel direction for each trial in all conditions. Once the participant was guided into the center of the pole, it disappeared and the trial would commence without any landmark information. In the no-vision conditions, this pole was the only visual information participants received during the trials. The pole's disappearance upon entry meant that no visual information was available during the loop closure task in the no-vision conditions. Thus, the start pole could not be used during the trial to indicate location in the environment, but was simply an anchor to mark what location should be tracked.

2.3. Loop closure task

In the loop closure task, an experimenter guided the participant in a circular trajectory. The participant clicked a wireless mouse once they thought that they had returned to the same place in which they had started, the home location. The experimenter continued walking in the circular trajectory until the participant clicked the mouse, even if they had passed the start location. We used three primary radii of interest for the loops: 1 m, 2 m, and 3 m (Fig. 1c). Participants experienced 12 trials of each of these radii for each condition (6 left and 6 right turning directions of each), divided pseudo-evenly over two experimental sessions. We also included three "filler" radii (0.5 m, 1.5 m, and 2.5 m) to prevent participants from learning the primary radii; each of these fillers were presented 4 times total in each condition (2 left and 2 right). The radii were presented in random order within each condition in each session, and trials alternated between left (counterclockwise) and right (clockwise) turning directions in the session.

Table 1
Experimental design. All conditions included vestibular information.

		Proprioception	
		Yes	No
Vision	Yes	Walk Vision (WalkV)	Wheelchair Vision (WheelV)
	No	Walk No Vision (WalkN-V)	Wheelchair No Vision (WheelN-V)

2.4. Experimental design

We crossed two levels of visual information (vision, no-vision) with two levels of proprioceptive information (walk, wheelchair) for a total of four experimental conditions (Table 1). The wheelchair no-vision (WheelN-V) condition only had vestibular information available to participants to track their movements and served as the baseline. The walking without vision (WalkN-V) and wheelchair with vision (WheelV) conditions each added one level of information onto the baseline. The walking with vision (WalkV) condition had all visual, proprioceptive, and vestibular information available to the participants. Through the use of this design, we tested how the addition of visual and proprioceptive information uniquely contribute to path integration. Furthermore, we could test whether the two types of information sum linearly or whether the inclusion of both types of information resulted in any interactions.

2.5. Procedure

Participants were instructed that they would be guided along circular paths. Participants were to click a button on the wireless mouse and inform the experimenter that they were ready for the next trial once they thought they had returned to the location where they began the trial (start location).

Each session began by fitting participants with the Oculus HMD and adjusting the HMD for comfort. Participants were given a brief VR task to familiarize them with virtual environments and to calibrate their

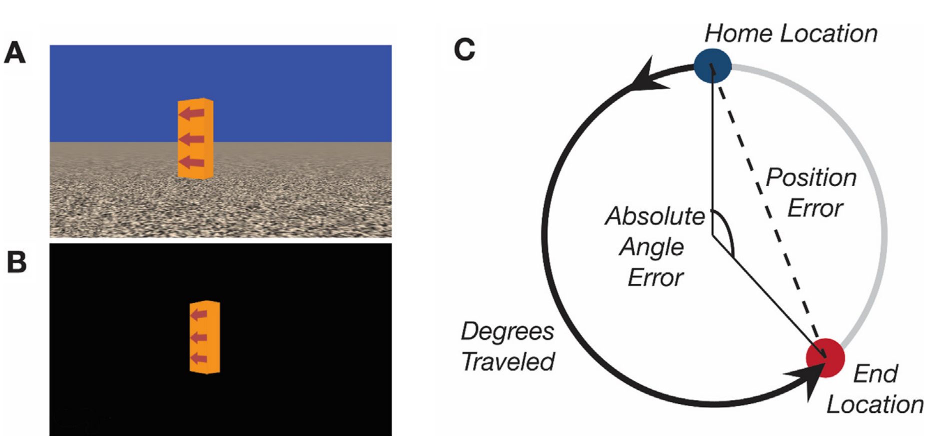

Fig. 1. (A) View of the virtual desert environment. The start pole indicates the home (start) location at the beginning of the trial. It disappears as soon as the participant enters it and cannot be used for localization. (B) View of the environment in the conditions without vision. The start pole was visible until entering, such that during the loop closure trial the visuals were all black. (C) Dependent measures from the loop closure task. Position error is the straight-line distance from the start location to the final position. Absolute angle error is the internal angle made between those two points, which normalizes for loop radius size. Degrees traveled is the sum of the degrees traveled on the circle. This measure both normalizes for loop radius size and indicates overshoots and undershoots.

visual and motor systems to the virtual environment. Four practice trials were given at the beginning of each session, one practice trial per condition (WalkV, WheelV, WheelN-V, WalkN-V), using radii from the filler list. Audio instructions of the task were delivered through headphones on the HMD for both the practice trials and experiment trials.

During the experiment, the experimenter led the participants on the circular paths. During walking conditions, the experimenter and participant linked arms at the elbow and walked side-by-side, while in wheelchair conditions the experimenter pushed the participant in a push wheelchair. All participants were guided at approximately the same speed, a normal walking speed of approximately 1.3 m/s, although some adjustments were made to accommodate participants with very fast or very slow natural walking speeds. Throughout, a secondary experimenter was tasked with keeping the cable for the HMD out of the way of the participant and the guiding experimenter. Lights in the room were kept off to minimize peripheral visual cues outside of the HMD. The guiding experimenter wore a head lamp to ensure their own ability to walk in the room. The experimenter used tape markings on the ground to guide participants around the correct radii; these markings were not visible to the participant.

The four experimental conditions were presented in blocks, with four blocks of 24 trials per block in each session. The order of the blocks was randomized in each session. The experiment was run in two sessions, each with 96 trials and 4 blocks (192 trials total), for a total of 48 trials in each condition over the course of the experiment. Brief breaks were taken in between each block in which participants could rest or have water. Each session lasted approximately 90 min.

At the end of the second session, participants were asked to report any strategies that they used in the task and to rate the difficulty of the four conditions on a 1–7 scale. Finally, participants completed several spatial abilities tasks, which allowed us to examine potential individual differences. These abilities tasks included the self-report questionnaire Santa Barbara Sense of Direction Scale (SBSOD) (Hegarty, Richardson, Montello, Lovelace, & Subbiah, 2002), a questionnaire about frequency and manner of personal video game use (modified from Terlecki & Newcombe, 2005), the Road Map Test in which participants reported the direction of each turn in a route pre-drawn on a city map (Money & Alexander, 1966; Zacks, Mires, Tversky, & Hazeltine, 2000), and the Perspective-Taking/Spatial Orienting Test in which participants viewed a 2D array of objects on a page and indicated directional relationships from imagined viewpoints (Kozhevnikov & Hegarty, 2001).

2.6. Data analysis

We analyzed the data using custom Python scripts, SPSS 24 (IBM), and R. Dependent measures (Fig. 1c) included (a) *total degrees traveled*, the actual number of degrees traversed around the circle, which can be compared to one complete loop, 360°, (b) *position error*, the straight-line distance between the location the participant marked as the home location and the actual home location, and (c) *absolute angular error*, the absolute value of the difference between the interior angle created by the participant's marked home location and the direction to the actual home location. The last two analyses involved unsigned (absolute) errors, so they could not be used to determine whether participants tended to undershoot or overshoot the home location. The total degrees traveled measure accounts for signed errors that would show overshoots and undershoots.

Because we used three different sized loops, position error was expected to become larger even when the proportion of the circle was the same. Absolute angular error normalizes across loop sizes because it is based on the interior angle, thus, any differences in absolute angular error related to loop size can be attributed to an effect of the path length. For position error and absolute angular error, chance was determined using the 90° point, since the participant could end anywhere between 0° and 180° in both directions, for an average value of 90°. Chance for position error was the straight-line distance between the home location and a position at the 90° point on a circle, which varied with each radius size.

Position error and absolute angular error involved unsigned (absolute) errors, so they could not be used to determine whether participants tended to undershoot or overshoot the home location, but they are the standard measures of accuracy in many path integration tasks. Total degrees traveled accounts for signed errors and is a way of distinguishing between small and large undershoots (or overshoots) that might have the same absolute angular error. The total degrees traveled was determined by marking each time the participant crossed through the initial axis they started at (after having left that location to start with) when traveling around the circle. Each complete circle added 360° to the total, with the remaining portion added to the final degree count. Determining a measure to account for signed errors proved to be surprisingly difficult, as simply summing the total distance traveled included side-to-side movement that artificially inflated the total and potentially caused differences between walking and wheelchair conditions. There is no meaningful indication of chance performance in this measure in terms of degrees traveled. However, we tested whether the data points for each participant were randomly distributed around a circle using a Rayleigh test for directionality using the Matlab CircStat toolbox (Berens, 2015). We further examined whether participants made severe undershoots (< 180°) or severe overshoots (> 540°). We additionally compared each condition with veridical performance, 360°.

Loops traveling to the left (counterclockwise) and right (clockwise) were collapsed in the analyses. Data collection error lead to the first 30 trials of one participant not being collected. Occasional trials were removed completely from the analyses for instances when the participant told us they had clicked earlier than intended, the participant become entwined in the cable, a trial was skipped by accident, or location tracking was lost. These errors occurred on approximately 4.50% of trials. In addition, on some trials the participant ended in the start location of the next trial by chance, triggering the start of data collection, leading to the recording of additional travel distance since they needed to turn around or get aligned with the correct direction. This occurred on approximately 1.73% of trials. However, since this extra distance did not affect the final position or the calculation of the total degrees traveled, they remained in the analysis. These trials were inspected manually for the total degrees traveled measure.

For position error and absolute angular error, we first conducted one-sample *t*-tests against chance values for each condition and radius size, whereas for total degrees traveled we conducted one-sample *t*-tests against 360°. We then conducted within-subjects repeated-measures ANOVAs for all three outcome measures with a 2 (walking/wheelchair) × 2 (vision/no vision) × 3 (radius size) design. Corrections for violations of sphericity were made where appropriate with the Greenhouse-Geisser correction. Significant effects were followed up with *post hoc* pairwise contrasts of the four conditions, using the Bonferroni method to correct for multiple comparisons. We also computed Bayes factors using R's BayesFactor package to compare the likelihood of the different models that incorporated the three factors of walking, vision, and radius, plus interactions. A Bayes factor indicates how much more likely each alternative model is supported compared with the null. Because our design was within-subject, we report comparisons between the experimental conditions + subject factors and a subject-only null model.

We further conducted a cue combination analysis on the within-subject measures of standard deviation. This analysis tested whether the cue averaging in these variable errors follows ideal weighting, using the Bayesian maximum likelihood estimation (MLE) model (Ernst & Banks, 2002; Landy et al., 1995). We first computed the ideal combined variance for the combined condition with both walking and vision (on top of the vestibular signal) for each participant using the equation

$$\sigma^2_{WalkVision} = \frac{\sigma^2_{Walk}\sigma^2_{Vision}}{\sigma^2_{Walk} + \sigma^2_{Vision}}$$

where σ^2_{Walk} is the variance from the WalkN-V condition and σ^2_{Vision} is the variance from the WheelV condition. From the computed ideal combined value $\sigma^2_{WalkVision}$for each participant, we took the square root to derive the standard deviation, and then compared the ideal value with the experimental standard deviation from the WalkV condition. We conducted a 2 (ideal/experimental) × 3 (radius size) ANOVA, followed by paired *t*-tests between the ideal MLE model and the experimental cue combined condition at each radius, Bonferroni corrected for multiple comparisons. We followed up by examining whether each participant had a higher experimental standard deviation compared with the MLE model. We then conducted a sign test (binomial test) to determine whether the number of participants with higher experimental values was greater than would be expected by chance.

We also examined the relationship between individual performance on the loop task in the different conditions with our spatial abilities tests. We conducted Pearson correlations relating performance in each condition and radius of the loop task with individual values on the SBSOD, Spatial Orienting Test (SOT), Road Map Test, and video game use questionnaire. Due to the exploratory nature of this analysis, we did not correct for multiple comparisons.

Finally, we analyzed participants' ratings of difficulty for each experimental task using a 2-way repeated-measures ANOVA (2 walk × 2 vision). We also examined participants' self-reported strategies for any regularities in how they performed the task.

3. Results

3.1. Degrees traveled

Fig. 2 shows individual trial data for all participants for all four conditions. For clarity, only the 2-m radius is illustrated in Fig. 2. The vast majority of trials (72.82%) for all radii and all conditions were less than one complete circle (0–360°). Most of the remaining trials (26.51%) were between one and two complete circles (360–720°), with only 0.67% of trials exceeding 720°. Overall, only 7.97% of trials were severe undershoots (i.e. less than ½ loop or < 180°), and 3.80% were severe overshoots (i.e. > 1½ loops or > 540°), meaning that over 88% of trials were within ± 180° of one complete loop. This result suggests that participants largely were aware of how many times they had traversed the circle, and that errors were not likely due to confusion about how many times they had circled (cf. Gallistel, 2018).

We conducted a Rayleigh test for random distribution on a circle for each participant for each condition and radius. In the WalkV condition, we found that 3 out of 23 participants were not different from random for the 1-m radius, while 4 and 6 participants were not different from random at the 2- and 3-m radii, respectively. The WalkN-V condition (1-m: 3 participants; 2-m: 6; 3-m: 6) and WheelV (1-m: 3 participants; 2-m: 4; 3-m: 7) had similar numbers of participants at chance. In contrast, in the WheelN-V condition 9 participants were random at all three radii.

Fig. 3a illustrates the mean results of the degrees traveled analysis. One-way ANOVAs against 360° – the ideal performance of one complete circle – found that the full-information WalkV condition was no different from ideal for the 2- and 3-m radii (2-m: $t_{22} = -1.322$, $p = 0.200$; 3-m: $t_{22} = -0.556$, $p = 0.584$), although it was different from ideal at the 1-m radius ($t_{22} = -2.379$, $p = 0.026$). The intermediate WalkN-V condition was also just over the threshold to not be different from 360° ($t_{22} = -2.058$, $p = 0.052$). The other two radii for the WalkN-V conditions and all three radii for the intermediate WheelV condition and the baseline vestibular only WheelN-V condition were significantly different from 360° for all radii (all $t < -2.5$, all $p < 0.05$). These results indicate that the WalkV condition was the closest to accurate, with substantial undershoots in the other three conditions.

We conducted a 2 (walking/wheelchair) × 2 (vision/no-vision) × 3 (radius size) repeated-measures ANOVA (Fig. 3a). We found a main effect of walking ($F_{1,22} = 26.717$, $p < 0.001$, $\eta^2_p = 0.548$) and a marginal main effect of vision ($F_{2,44} = 3.437$, $p = 0.077$, $\eta^2_p = 0.135$), but no main effect of radius ($F_{1,22} = 0.156$, $p = 0.739$, $\eta^2_p = 0.007$). There was also a significant vision × radius interaction ($F_{1,22} = 10.719$, $p = 0.001$, $\eta^2_p = 0.327$). Critically, there was no interaction between vision and walking ($F_{1,22} = 2.817$, $p = 0.107$, $\eta^2_p = 0.114$). The remaining interactions were also not significant ($p > 0.6$).

Post-hoc pair-wise comparisons showed that the WalkV condition had greater degrees traveled than both the WheelV ($p < 0.001$, Bonferroni corrected) and WheelN-V ($p = 0.003$, Bonferroni corrected) conditions, and but was not higher than the WalkN-V condition ($p = 0.104$, Bonferroni corrected). The WalkN-V was significantly higher than the WheelN-V condition ($p = 0.035$, Bonferroni corrected), but was not different from the WheelV condition ($p = 1.000$, Bonferroni corrected). Together, these results indicate that walking had improved performance compared with vestibular only. Vision increasingly improved performance in larger circles, whereas the restriction of vision led to increasing undershoots. The lack of interaction between vision and walking and no pairwise difference between the WalkN-V and WheelV conditions suggests that these two factors contributed equally to performance in the loop closure task.

The Bayes Factor analysis showed that the main effect of walking + subject had a BF of 2.68×10^5 (± 2.41%), the main effect of vision + subject had a BF of 12.15 (± 1.14), and the main effect of radius + subject had a BF of 0.05 (± 0.96%). The model with the greatest support included the factors of walking + vision + subject, but not radius or interactions, with a BF of 6.51×10^6 (± 11.98%). These results indicate that both walking and vision made contributions in this task.

The within-subject standard deviations, a measure of consistency and variability, (Fig. 3b) found a main effect of vision ($F_{1,22} = 9.500$, $p = 0.005$, $\eta^2_p = 0.302$) and a main effect of radius ($F_{2,44} = 11.355$, $p = 0.001$, $\eta^2_p = 0.340$), as well as a marginal main effect of walking ($F_{1,22} = 4.232$, $p = 0.052$, $\eta^2_p = 0.161$), but no interactions (all $p > 0.3$). Pair-wise comparisons between the four conditions found the WalkV and WheelV condtions had lower variability than the WheelN-V condition (WalkV: $p = 0.013$; WheelV: $p = 0.046$, Bonferroni corrected, all other $p > 0.2$). Together, these results indicate that performing the loop closure task without vision was associated with increased variability, while larger loop sizes also had higher variability.

The final analysis for the degrees traveled examined the combination of visual and proprioceptive cues. There was a main effect of cue combination (ideal vs. experimental) ($F_{1,22} = 13.157$, $p = 0.001$, $\eta^2_p = 0.374$) and radius ($F_{2,44} = 10.383$, $p = 0.001$, $\eta^2_p = 0.321$), but no cue × radius interaction ($F_{2,44} = 0.448$, $p = 0.629$, $\eta^2_p = 0.0.020$). The post-hoc pairwise tests between the MLE model and the experimental data for each radius showed differences at the 2-m and 3-m radii (2 m: $p = 0.039$; 3 m: $p = 0.042$, Bonferroni corrected). The lower cue combination values in the MLE model compared with the WalkV data suggest that navigators did not optimally combine these cues.

We further examined the cue combination results on an individual basis. We computed the number of times, over 23 participants and for each radius, in which the experimental data from the WalkV condition was greater than the MLE predicted values. For the 1-m radius, we found that 15 of the 23 participants had greater deviations in the experimental data. This result was not different from chance (Sign test: $p = 0.211$). However, for both the 2-m ($p = 0.035$) and 3-m ($p = 0.035$) radii, 17 participants had greater deviations in the experimental data, which was significantly different from chance.

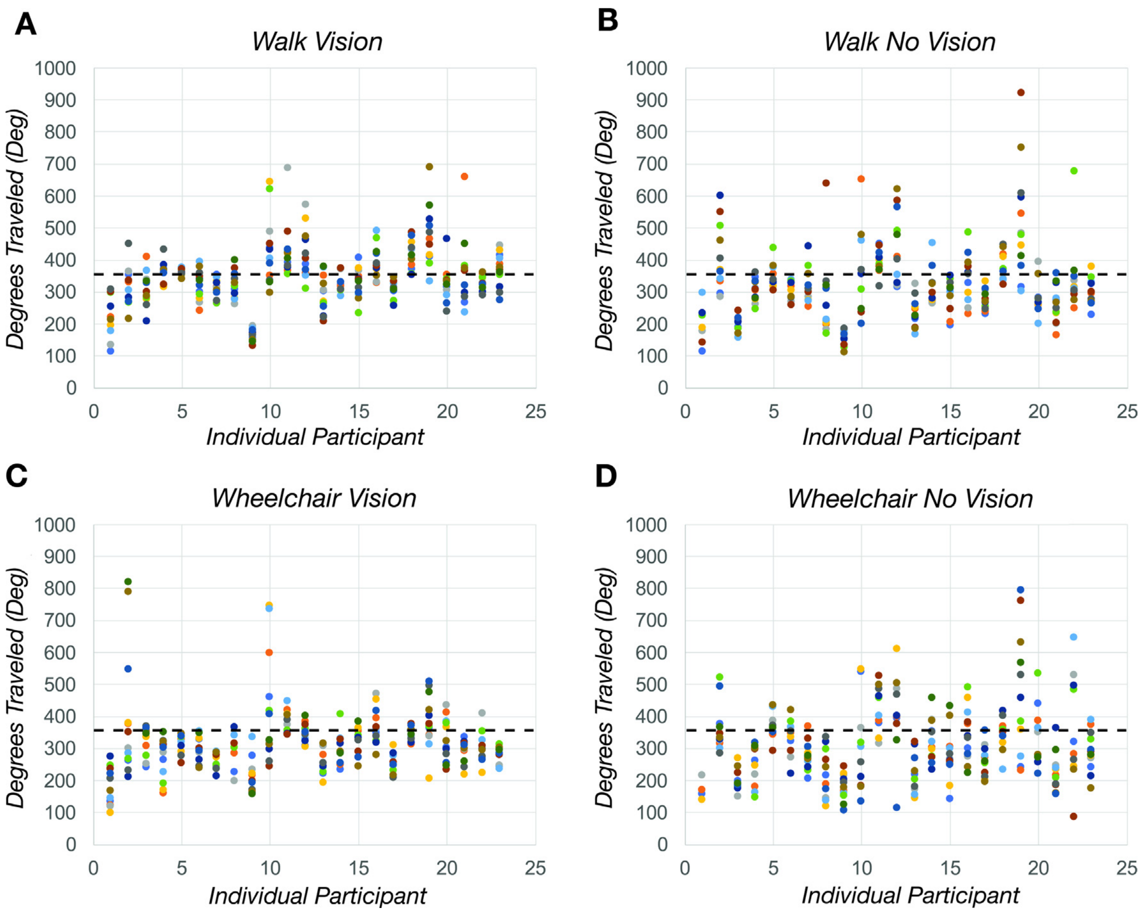

Fig. 2. Total degrees traveled, individual performance. For simplicity, only the 2-m radius is illustrated for each condition. All 12 trials (omitting any bad trials) for each of the 23 participants is shown in each condition. The dashed line indicates ideal performance for one loop (360°). (A) Walk Vision (WalkV) condition. (B) Walk No Vision (WalkN-V) condition. (C) Wheelchair Vision (WheelV) condition. (D) Wheelchair No Vision (WheelN-V) condition.

3.2. Position error

The results for position error are shown in Fig. 4a. Position error was first compared against chance for all conditions and for all radii. Chance differed for each radius because the straight-line distance to the home location is further for a larger circle. The test levels for chance were 1.414 m, 2.828 m, and 4.243 m for the 1, 2, and 3-m radius circles, respectively. One-sample *t*-tests against chance indicated that all three radii for the full-information condition WalkV were significantly better than chance (1-m: $t_{22} = -7.339$, $p < 0.001$; 2-m: $t_{22} = -7.064$, $p < 0.001$; 3-m: $t_{22} = -6.668$, $p < 0.001$). The intermediate condition WalkN-V was better than chance for all radii (1-m: $t_{22} = -4.202$, $p < 0.001$; 2-m: $t_{22} = -3.163$, $p = 0.005$; 3-m: $t_{22} = -2.165$, $p = 0.041$), as was the WheelV condition (1-m: $t_{22} = -4.460$, $p < 0.001$; 2-m: $t_{22} = -4.860$, $p < 0.001$; 3-m: $t_{22} = -3.086$, $p = 0.005$). In contrast, the baseline condition with vestibular information only, WheelN-V, was only significantly better than chance at the 1-m radius (1-m: $t_{22} = -2.211$, $p = 0.038$; 2-m: $t_{22} = -1.670$,

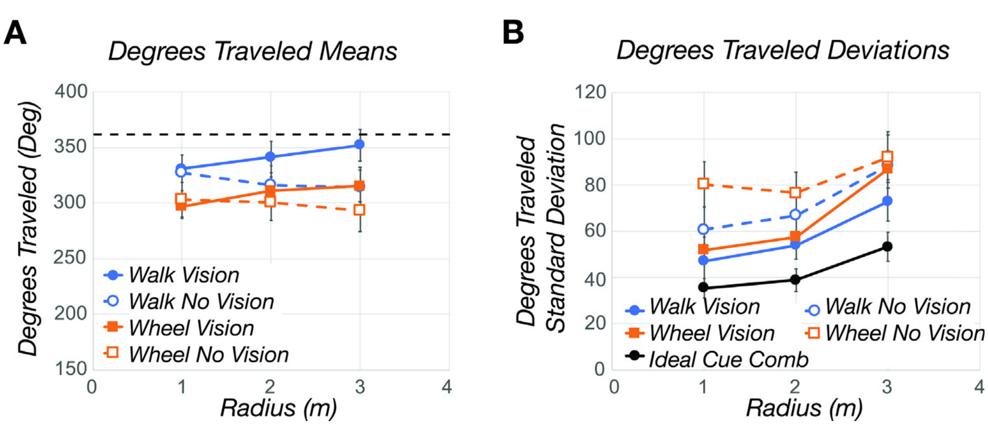

Fig. 3. Total degrees traveled. (A) Means for all conditions and radii. A significant main effect of walking ($p < 0.001$) and a significant vision × radius interaction ($p = 0.001$) were found. Dashed line indicates ideal performance for one loop (360°). (B) Within-subject standard deviations for all conditions and radii. This analysis found a main effect of vision ($p = 0.005$) and a main effect of radius ($p = 0.001$), with a marginal effect of walking ($p = 0.052$). The ideal combination of the walking and vision cues from the MLE model is shown in black. The data from the WalkV condition had significantly higher standard deviations than the model ($p = 0.001$ for MLE vs. experimental), indicating the cues were not ideally combined. Error bars indicate one standard error of the mean.

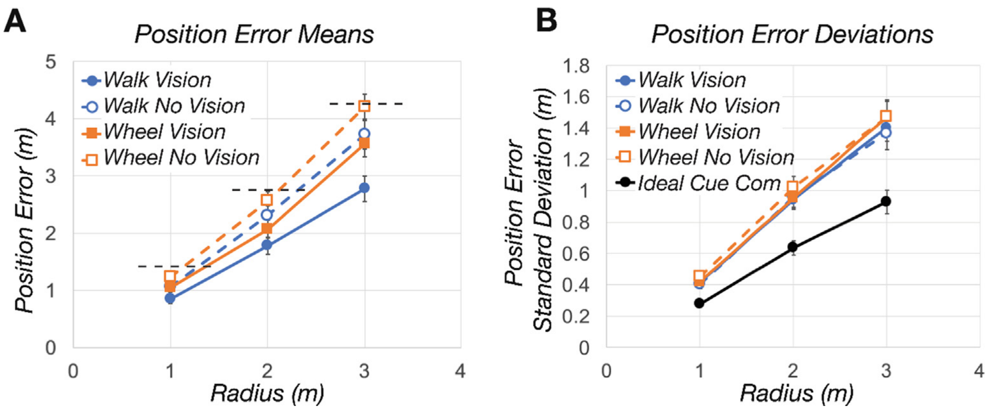

Fig. 4. Position error. (A) Means for all conditions and all radii. Position errors had a significant main effect of walking ($p = 0.001$), a main effect of vision ($p < 0.001$), and a main effect of radius ($p < 0.001$). There were interactions with radius, but no interactions between walking and vision. The dashed line indicates chance values. Chance differs for the three radii because the straight-line distance for a larger circle is greater than for a smaller circle at the same point in terms of degrees. (B) Within-subject standard deviations for all conditions and all radii. There was a significant main effect of radius ($p < 0.001$), but no effects of walking, vision, or interactions. The ideal combination of the walking and vision cues from the MLE model is shown in black. The data from the WalkV condition had significantly higher standard deviations than the model, indicating the cues were not ideally combined. Error bars indicate one standard error of the mean.

$p = 0.109$; 3-m: $t_{22} = -0.204$, $p = 0.840$). These findings demonstrate that vestibular information was not sufficient to perform the loop closure task, but that visual and proprioceptive information were sufficient individually.

We next conducted a 2 (walking/wheelchair) × 2 (vision/no-vision) × 3 (radius size) repeated-measures ANOVA on the mean errors. This analysis found a main effect of walking ($F_{1,22} = 16.150$, $p = 0.001$, $\eta_p^2 = 0.423$), a main effect of vision ($F_{1,22} = 23.763$, $p < 0.001$, $\eta_p^2 = 0.519$), and a main effect of radius ($F_{2,44} = 342.088$, $p < 0.001$, $\eta_p^2 = 0.940$). Critically, there was no interaction between walking and vision ($F_{1,22} = 0.875$, $p = 0.360$, $\eta_p^2 = 0.038$) and no three-way interaction ($F_{2,44} = 1.098$, $p = 0.325$, $\eta_p^2 = 0.048$). There was an interaction between walking and radius ($F_{2,44} = 9.225$, $p = 0.001$, $\eta_p^2 = 0.295$) and between vision and radius ($F_{2,44} = 8.525$, $p = 0.003$, $\eta_p^2 = 0.279$). The main effect of radius was expected due to larger radii having larger potential errors. However, the interactions between radius and walking and between radius and vision suggests that the lack of other information can exaggerate the radius effects.

Follow-up pairwise comparisons between the four experimental conditions indicated that the WalkV condition had significantly lower position errors than all other conditions (compared with WalkN-V: $p < 0.001$, WheelV: $p = 0.025$, WheelN-V: $p < 0.001$; all p-values Bonferroni corrected). The WheelN-V had significantly higher errors than all other conditions (compared with WalkN-V: $p = 0.009$, WheelV: $p = 0.015$, all p-values Bonferroni corrected). The two intermediate conditions, WalkN-V and WheelV were no different from each other (uncorrected $p = 0.348$, Bonferroni corrected $p = 1.000$). Together, these findings suggest that proprioceptive information from walking and visual optic flow information both contribute to accuracy in the loop closure task. Similar to degrees traveled, the lack of interaction or differences between WalkN-V and WheelV conditions suggests that vision and walking contributed equally to performance in the loop closure task.

Further tests incorporating the Bayes Factor (BF) demonstrated strong support for all three of our factors (walking, vision, and radius). The contribution of just the walking factor + subject added the least over the subject-only model, 2.17 (± 0.76%), with the vision factor + subject having a BF of 29.16 (± 0.79%). However, radius + subject was the largest contributing single factor, with a BF of 1.69×10^{68} (± 0.70%). The model with the largest BF included the main effects of walking, vision, and radius, plus a walking × radius interaction and a vision × radius interaction + subject. The BF for this model was 2.19×10^{82} (± 5.64%). These findings confirm that radius is a major factor in position error, as expected, but also demonstrate strong support for vision and walking making independent contributions.

For the within-subject standard deviations (Fig. 4b), we found a main effect of radius ($F_{2,44} = 286.194$, $p < 0.001$, $\eta_p^2 = 0.929$), but no main effect of walking ($F_{1,22} = 1.431$, $p = 0.244$, $\eta_p^2 = 0.061$) or of vision ($F_{1,22} = 0.048$, $p = 0.829$, $\eta_p^2 = 0.002$) and no interactions (all $p > 0.5$). These findings indicate that only radius size played a role in consistency.

The cue combination analysis found a significant effect difference between WalkV condition and the predicted cue combination standard deviation from the MLE model ($F_{1,22} = 35.121$, $p < 0.001$, $\eta_p^2 = 0.615$), as well as an effect of radius ($F_{2,44} = 150.638$, $p < 0.001$, $\eta_p^2 = 0.873$) and a cue combination × radius interaction ($F_{2,44} = 13.883$, $p < 0.001$, $\eta_p^2 = 0.387$). Post-hoc pairwise *t*-tests showed that the ideal MLE predicted model had significantly lower standard deviations than the experimental data from the WalkV condition for all three radii ($p < 0.001$, Bonferroni corrected for all radii). These findings suggest that despite fairly equal contributions to variability from walking and vision, the navigators did not combine these two cues in an ideal manner.

Individual analysis of the cue combination data showed that for all three radii, more participants than expected by chance had greater position error deviations than the MLE prediction. For the 1-m radius, 17 participants had higher deviations (Sign test: $p = 0.035$), for the 2-m radius, 19 participants had higher deviations ($p = 0.003$), and for the 3-m radius, 20 participants had higher experimental deviations ($p = 0.001$).

3.3. Absolute angular error

Fig. 5a shows the results for absolute angular errors. We first tested the mean absolute angular errors against chance. Angular error was normalized across all radius sizes because chance is 90° for all loops. One-way *t*-tests against chance found that all three radii for the full-information condition WalkV were significantly better than chance (1-m: $t_{22} = -4.975$, $p < 0.001$; 2-m: $t_{22} = -4.855$, $p < 0.001$; 3-m: $t_{22} = -4.309$, $p < 0.001$). In contrast, the baseline condition of WheelN-V was not significantly different from chance for the 1- and 2-m radii and was significantly worse than chance for the 3-m radius (1-m: $t_{22} = 0.254$, $p = 0.802$; 2-m: $t_{22} = 0.321$, $p = 0.751$; 3-m: $t_{22} = 2.173$, $p = 0.041$). The intermediate conditions of WalkN-V (1-m: $t_{22} = -2.635$, $p = 0.015$; 2-m: $t_{22} = -1.317$, $p = 0.201$; 3-m: $t_{22} = -0.126$, $p = 0.901$) and WheelV (1-m: $t_{22} = -2.258$, $p = 0.034$; 2-m: $t_{22} = -3.272$, $p = 0.003$; 3-m: $t_{22} = -1.197$, $p = 0.244$) had some radii better than chance and some no different from chance. These results suggest that vestibular information was not sufficient to perform the loop closure task. The results also suggest that the addition of visual and proprioceptive information individually facilitated performance

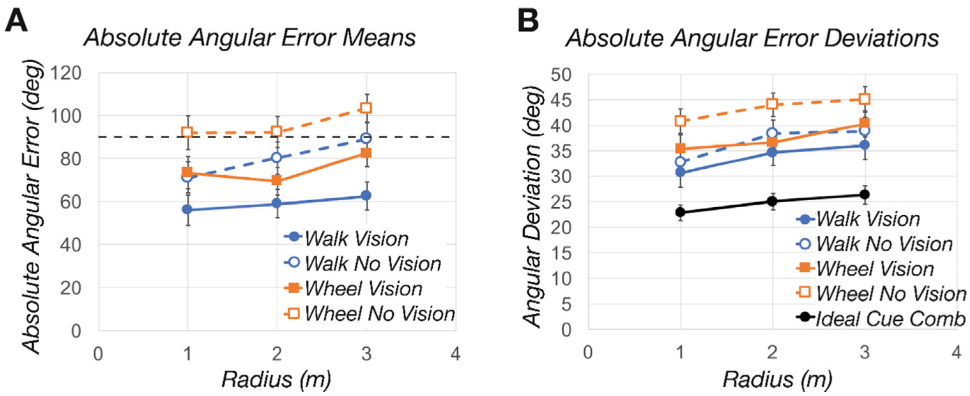

Fig. 5. Absolute (unsigned) angular errors. (A) Means for all conditions and radii. This analysis found significant main effects of walking ($p < 0.001$), vision ($p < 0.001$), and radius ($p = 0.003$) and no interactions. The dashed line indicates chance values, which is 90° for all circle sizes. (B) Within-subject angular deviations for all conditions and radii. There was a significant main effect of walking ($p = 0.004$), a main effect of vision ($p = 0.017$), and of radius ($p = 0.001$) and no interactions. The ideal combination of the walking and vision cues from the MLE model is shown in black. The data from the WalkV condition had significantly higher angular deviations than the model, indicating the cues were not ideally combined. Error bars indicate one standard error of the mean.

somewhat, but only the inclusion of both visual and proprioceptive information was sufficient for non-random performance for all radii.

We next conducted a 2 (walking/wheelchair) × 2 (vision/no-vision) × 3 (radius size) repeated-measures ANOVA. We found a significant main effect of walking ($F_{1,22} = 18.808$, $p < 0.001$, $\eta_p^2 = 0.461$), a main effect of vision ($F_{1,22} = 22.174$, $p < 0.001$, $\eta_p^2 = 0.502$), and a main effect of radius ($F_{2,44} = 8.061$, $p = 0.003$, $\eta_p^2 = 0.268$). There was no walk × vision interaction ($F_{1,22} = 0.002$, $p = 0.961$, $\eta_p^2 = 0.000$) and no 2- or 3-way interactions with radius (all $p > 0.1$). The significant effect of radius suggests that even when normalizing for radius size, larger loops have higher errors.

We followed up with pair-wise comparisons between the four conditions. The WalkV condition had significantly lower absolute angular errors than all three other conditions (compared with WalkN-V: $p = 0.001$, WheelV: $p = 0.025$, WheelN-V: $p < 0.001$, all p-values Bonferroni corrected). The vestibular-only WheelN-V condition had significantly higher errors than the other conditions (compared with WalkN-V: $p = 0.001$, WheelV: $p = 0.005$, all p-values Bonferroni corrected). The two intermediate conditions, WalkN-V and WheelV were no different from each other (uncorrected $p = 0.421$, Bonferroni corrected $p = 1.000$). These results suggest that proprioceptive information from walking and visual optic flow information both contribute to accuracy in the loop closure task. The lack of interaction between vision and walking and no pairwise difference between the WalkN-V and WheelV conditions suggests that these two factors contributed equally to performance in the loop closure task.

The Bayes Factors model with the most support included the main effects of walking + vision + radius + subject with no interactions ($BF = 1.83 \times 10^{19}$ [± 1.62%]). For single factors, the main effect of walking + subject had a BF of 2.47×10^5 (± 3.04%), the main effect of vision + subject had a BF of 3.80×10^{10} (± 3.08%), and the main effect of radius + subject had a BF of 5.56 (± 0.77%). Thus, when normalizing across loop sizes, radius still had substantial impact, but walking and vision were even stronger factors. The strong support for separate factors suggests that walking, vision, and radius size make independent contributions to this task.

The within-subject standard deviations of absolute angular error showed a significant main effect of walking ($F_{1,22} = 10.365$, $p = 0.004$, $\eta_p^2 = 0.320$), a main effect of vision ($F_{1,22} = 6.694$, $p = 0.017$, $\eta_p^2 = 0.233$), and a main effect of radius ($F_{2,44} = 8.570$, $p = 0.001$, $\eta_p^2 = 0.280$) (Fig. 5b). There was no interaction between vision and walking ($F_{1,22} = 0.816$, $p = 0.376$, $\eta_p^2 = 0.036$) and no 2- or 3-way interactions with radius (all $p > 0.5$). These findings indicate that all three factors contributed to within-subject variability of absolute angular errors.

The cue-combination analysis for the angular deviations found a significant main effect of cue (ideal vs. experimental) ($F_{1,22} = 16.594$, $p = 0.001$, $\eta_p^2 = 0.430$) and a significant effect of radius ($F_{2,44} = 5.085$, $p = 0.012$, $\eta_p^2 = 0.188$), but no interaction ($F_{2,44} = 0.321$, $p = 0.659$, $\eta_p^2 = 0.014$). Post-hoc pairwise *t*-tests (Bonferroni corrected) between the MLE model predicted ideal cue combination and the experimental standard deviation from the WalkV condition found significantly lower standard deviations in the MLE model than the experimental data at the 1-m ($p = 0.036$), 2-m ($p = 0.003$) and 3-m ($p = 0.003$) radii. These results indicate that people generally did not combine the walking and vision cues in an ideal fashion.

We examined the cue combination results for absolute angular error on an individual basis as well. The 1-m radius had 15 people with higher experimental deviations, which was no different from chance using a sign test ($p = 0.211$). The 2-m (18 participants, Sign: $p = 0.011$) and 3-m (17 participants, Sign: $p = 0.035$) radii had significantly more individuals with higher deviations than the MLE than would be expected by chance.

3.4. Individual differences

We conducted Pearson correlations between performance on the loop closure task and several self-report and spatial abilities measures. Spatial Orienting Test (SOT) scores were not collected for two participants. Due to the exploratory nature of these tests, we did not correct for multiple comparisons in these correlations. The years playing video games measure was not correlated with any outcome measure.

For the total loop degrees traveled measure, only one negative correlation between and SBSOD (higher scores on the SBSOD indicate worse sense of direction) and WheelN-V ratio (1-m radius: $r_{21} = -0.529$, $p = 0.009$) was observed, indicating that people with worse sense of direction tended to undershoot more.

For the full information WalkV condition, correlations were found between scores on the SBSOD and position errors at all radii (1-m radius: $r_{21} = 0.486$, $p = 0.019$; 2-m radius: $r_{21} = 0.429$, $p = 0.041$; 3-m radius: $r_{21} = 0.420$, $p = 0.046$), indicating that people with better sense of direction had lower errors. In WalkV, there was a somewhat surprising negative correlation with errors in the SOT (3-m radius: $r_{19} = -0.455$, $p = 0.038$) and a positive correlation with road map scores (3-m radius: $r_{21} = 0.428$, $p = 0.041$) with position error. These results indicate that better performance on those spatial measures were associated with greater position errors. None of the factors was correlated with the WalkN-V condition. SBSOD was also correlated with position errors in the WheelV (1-m radius: $r_{21} = 0.539$, $p = 0.008$; 2-m radius: $r_{21} = 0.441$, $p = 0.035$) and WheelN-V (1-m radius: $r_{21} = 0.478$, $p = 0.021$; 2-m radius: $r_{21} = 0.475$, $p = 0.022$) conditions. Fig. 6 illustrates several of the relationships between position error and the spatial abilities measures.

The findings observed for absolute angular errors were similar to those of position errors. Most of the correlations were with the SBSOD,

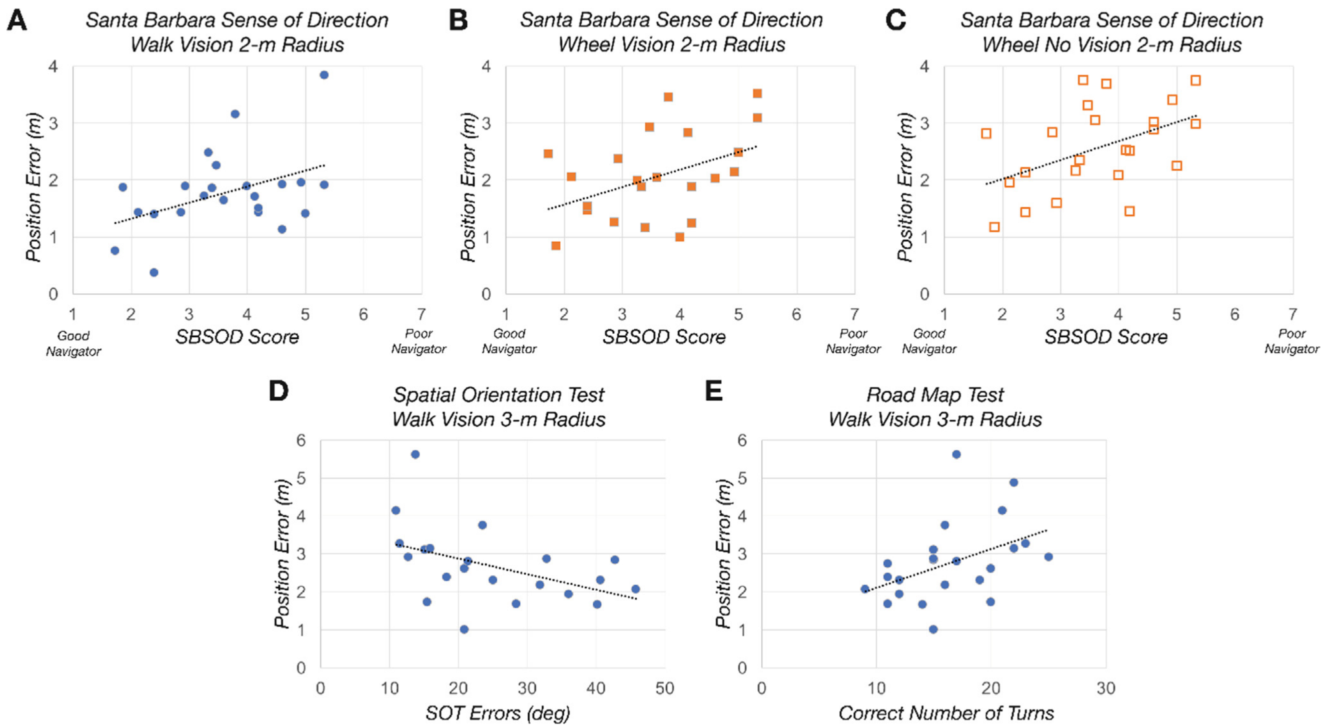

Fig. 6. Individual differences in performance in the loop closure task. The Santa Barbara Sense of Direction Scale was significantly positively correlated with position errors in several conditions, including (A) WalkV, 2-m radius ($r_{21} = 0.429$, $p = 0.041$), (B) WheelV, 2-m radius ($r_{21} = 0.441$, $p = 0.035$), and WheelN-V, 2-m radius ($r_{21} = 0.475$, $p = 0.022$). This relationship indicates that people with worse self-reported sense of direction (higher score) had greater position errors. For the 3-m radius of WalkV, relationships were observed with both the (D) Spatial Orientation Test ($r_{19} = -0.455$, $p = 0.038$) and the (E) Road Map Test ($r_{21} = 0.428$, $p = 0.041$), such that people who performed better on those tests had worse position errors. Dotted lines indicate linear fit of the data.

indicating that people with better self-reported sense of direction had lower absolute angular errors. This pattern held and the 1- and 2-m radii for the WalkV condition (1-m radius: $r_{21} = 0.494$, $p = 0.017$; 2-m radius: $r_{21} = 0.419$, $p = 0.046$), WheelV condition (1-m radius: $r_{21} = 0.515$, $p = 0.012$; 2-m radius: $r_{21} = 0.415$, $p = 0.049$), and WheelN-V condition (1-m radius: $r_{21} = 0.465$, $p = 0.025$; 2-m radius: $r_{21} = 0.468$, $p = 0.024$), but not for the WalkN-V condition. An additional negative correlation was observed between SOT and WalkV angular errors (3-m radius: $r_{19} = -0.441$, $p = 0.045$).

3.5. Difficulty ratings

Participants rated the difficulty of the four conditions on a 1–7 scale, with 1 being the easiest and 7 the most difficult. Mean ratings are shown in Fig. 7. A 2 (walk/wheel) × 2 (vision/no-vision) repeated-measures ANOVA found a significant main effect of vision on ratings ($F_{1,22} = 56.093$, $p < 0.001$, $\eta_p^2 = 0.728$), with conditions with vision rated significantly easier than those without vision. There was no effect of walking ($F_{1,22} = 1.355$, $p = 0.257$, $\eta_p^2 = 0.061$) and no interaction ($F_{1,22} = 0.000$, $p = 1.000$, $\eta_p^2 = 0.000$). These results indicate that the removal of vision made the subjective experience of the loop closure task much more difficult.

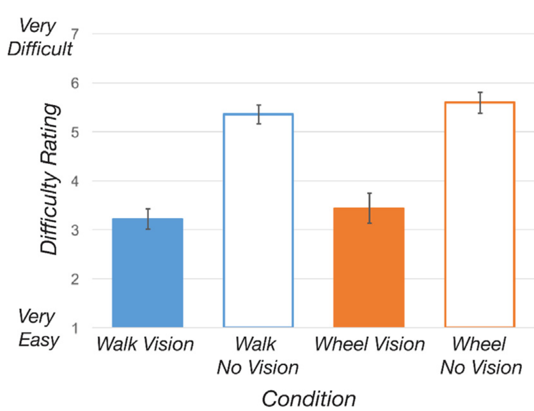

Fig. 7. Self-reported ratings for the difficulty of the four experimental conditions. A significant main effect of vision was found ($p < 0.001$), with conditions with vision rated as significantly easier than conditions without vision.

3.6. Strategies

We also asked participants about their strategies in completing the tasks. 13 participants reported using at least one strategy that involved visualization of the circle and path, most with mental imagery but a few with envisioning the circle on the ground. These visualizations sometimes included trying to split the circle into four quadrants. Five participants reported trying to track the location of the start pole of where the start pole had been, either by keeping track of their orientation and returning to that orientation or by tracking an imagined circle on the ground. Other strategies included using physical cues from their step size and angle, using cardinal directions, or using the horizon background to orient. Only one participant reported an attempt to count steps, but they found it distracting and moved to a mental imagery strategy.

4. Discussion

In this study, we used a novel loop closure task to test the contributions of vestibular, visual, and proprioceptive information during path integration. Contrary to previous research, we found that vestibular information alone led to chance performance, while visual optic flow and proprioception made relatively equal and independent contributions. However, these two cues were not integrated in a Bayesian ideal manner. Despite their relatively equal contributions, participants rated conditions without vision as much more difficult than conditions without proprioception. Performance was worse with larger radii, indicating a drift in the path integration system. We also observed large individual differences in performance, such that better performance was correlated with better self-reported sense of direction, but surprisingly, with worse perspective taking. Together, these findings demonstrate the importance of both vision and proprioception to human path integration.

4.1. Proprioceptive and visual information make equal contributions to loop closure

Our findings of equal contributions of vision and proprioception run counter to previous research suggesting that body-based cues dominate over visual cues (Campos et al., 2010; Chance et al., 1998; Kearns et al., 2002; Klatzky et al., 1998; Ruddle & Lessels, 2009). Our results also do not agree with studies that found that the addition of proprioception makes little contribution over purely vestibular input (Allen et al., 2004; Campos et al., 2012; Ehinger et al., 2014); our vestibular only condition was at chance whereas vestibular + proprioception had significantly lower errors. Some previous research has also indicated that vestibular information from physical turns is sufficient for successful path integration (Chance et al., 1998; Klatzky et al., 1998; Riecke, Bodenheimer, McNamara, Williams, Peng, & Feuereissen, 2010), but we found no evidence that vestibular information played a role in our task. However, the physical turns in previous studies were turns made in place, rather than curved trajectories. Our findings of a strong contribution from vision suggest that desktop VR that only uses visual information is sufficient for path integration, but given that proprioception makes an equal contribution, it seems prudent to include idiothetic cues whenever possible.

Differences between triangle completion and loop closure tasks could explain these discrepancies. Triangle completion is characterized by a single rotation in place during the outbound path. In contrast, loop closure involves continuous rotation along the circle. Since the inner ear detects *changes* in rotation and linear *acceleration*, our fairly constant speed and gentle curves may have precluded a strong vestibular contribution. We have not yet directly compared loop closure to triangle completion, so the exact relationship between these tasks is yet unknown. Although loop closure was designed to circumvent the limitations of triangle completion, it also restricts participants to a predetermined loop shape. With these considerations, the effects of body-based information on triangle completion could stem from the production of the homebound response. The lack of free movement trajectories, for which there is mixed evidence (Philbeck et al., 2001; Wan, Wang, & Crowell, 2010), could also explain these effects. Thus, the significance of the loop closure task may require additional testing to be fully determined.

We also compared our results to studies of survey knowledge, due to the theorized importance of path integration for survey knowledge acquisition (Gallistel, 1990; Wang, 2016). Our results are consistent with previous studies that show a strong contribution from walking but limited contribution of vestibular information to the acquisition of survey knowledge (Chrastil & Warren, 2013; Ruddle, Volkova, & Bülthoff, 2011; Waller & Greenauer, 2007; Waller, Loomis, & Haun, 2004; Waller, Loomis, & Steck, 2003). This finding supports the view that path integration could be the underlying mechanism for survey knowledge. However, none of those survey knowledge studies tested vestibular or proprioceptive information alone; instead, they typically used visual information as the baseline. Thus, the critical question of the contributions of vestibular or proprioceptive information alone to survey knowledge remains unknown.

Finally, the results of the mean degrees traveled have a somewhat different pattern compared with the position error and absolute angular error results. The degrees traveled means showed closer to ideal performance for the walking conditions, whereas the associated wheelchair conditions had underestimates consistently across all radii. Interestingly, the conditions with vision showed increasing degrees traveled with increasing radius, but the conditions without vision had decreasing degrees traveled in larger circles. It is possible that walking tends to improve the estimation of distances across the board, whereas the lack of vision leads to more conservative estimates at longer distances and to increased variability. However, the variability and cue combination results for the degrees traveled ratio were similar to the other measures. Overall, these findings still support relatively equal and independent contributions of vision and proprioception.

4.2. Cues are not combined in an optimal Bayesian manner

Our results indicate that cue combination of visual optic flow and body-based information was not ideal, even with equal contributions of these factors. We note that Bayesian cue combination is most beneficial when the variance thresholds for each cue are roughly equal. This pattern held for most participants, but instances of different variance thresholds could affect the combined averages. Thus, we reported the individual results as well, which largely showed that more participants than expected by chance had greater experimental deviations than MLE-predicted deviations.

Our findings are consistent with the adult data from Petrini et al. (2016) of non-optimal weighing for path reproduction. However, our results conflict with optimal weighing in Petrini's child data and with findings from a distance estimation task (Campos et al., 2010). Those tasks involved non-homing path integration, so the task could underlie this difference. However, evidence from homing in triangle completion suggests that the cues are combined in some way, although it is unclear how optimally (Tcheang et al., 2011). It is also possible that children weigh cues without preconceived ideas about reliability, whereas adults might bring up cognitive strategies that interfere with ideal cue combination.

We found that people rated conditions without vision as substantially more difficult than conditions without proprioception, even though their performance data suggest that these two cues made equal contributions. This result could help explain why the Bayesian cue combination analysis did not reveal ideal weighting: people might weigh the visual cues more strongly. These results indicate that introspection on the cues used for the task does not match their actual contribution.

4.3. Individuals differ in their path integration abilities

We found substantial individual differences in loop closure performance, which were related to self-reported sense of direction and to perspective taking abilities. In our previous fMRI study, we found no relationship between the loop task and either of these factors, although we did find connections with brain structure and function (Chrastil, Sherrill, Aselcioglu, Hasselmo, & Stern, 2017; Izen, Chrastil, & Stern, 2018). However, that experiment had a coarser outcome measure, highlighting the importance of the fine-grained error measures that we used in the present study. Few, if any, prior studies have found a relationship between path integration performance and other measures of spatial abilities.

Better self-reported sense of direction in the SBSOD was associated with lower position and angular errors in three of the four conditions, but we cannot make a conclusive assessment of how individual abilities interact with the available cues. However, this result does indicate that self-reported ability is related to path integration skill, and not just landmark-based navigation (Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006). The surprising result that better performance in the two perspective taking tasks was linked with worse errors in loop closure suggests that path integration ability is distinct from other types of navigation. Indeed, our results suggest that using perspective taking as a strategy in this task could actually make performance worse.

In sum, the loop closure task reveals novels ways to study path integration, which contrast the traditional triangle completion paradigm. Several new questions have emerged from this approach, opening up avenues for future study.

Supplementary material

The data and analysis scripts for this study are archived and publicly available on Open Science Framework at https://osf.io/3xgkd/ to comply with the data sharing policies of this journal.

Author contributions

E.C. developed the idea and designed the experiments. E.C. and G.N. developed the stimuli and coded the experiment. G.N., E.C, and A.H. collected the data. A.H., E.C., and G.N. performed data analysis. E.C. and G.N. wrote the manuscript. All authors approved the final version of the manuscript for submission.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cognition.2019.06.010.

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