

How You Get There From Here: Interaction of Visual Landmarks and Path Integration in Human Navigation

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Abstract

How do people combine their sense of direction with their use of visual landmarks during navigation? Cue-integration theory predicts that such cues will be optimally integrated to reduce variability, whereas cue-competition theory predicts that one cue will dominate the response direction. We tested these theories by measuring both accuracy and variability in a homing task while manipulating information about path integration and visual landmarks. We found that the two cues were near-optimally integrated to reduce variability, even when landmarks were shifted up to 90°. Yet the homing direction was dominated by a single cue, which switched from landmarks to path integration when landmark shifts were greater than 90°. These findings suggest that cue integration and cue competition govern different aspects of the homing response: Cues are integrated to reduce response variability but compete to determine the response direction. The results are remarkably similar to data on animal navigation, which implies that visual landmarks reset the orientation, but not the precision, of the path-integration system.

Keywords

navigation, Bayesian integration, cue competition, path integration, visual landmarks

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Humans share two fundamental navigation mechanisms with other animals. One is the path-integration system, the sense of direction that keeps track of one's position and orientation based primarily on self-motion information from the body senses (Etienne & Jeffery, 2004; Kearns, Warren, Duchon, & Tarr, 2002; Loomis et al., 1993). Another is the landmark-guidance system, which relies on visual landmarks and other environmental information for homing, reorientation, and way finding (Collett, 2010; Trullier, Wiener, Berthoz, & Meyer, 1997). Theoretically, navigational cues detected by the landmark-guidance system and the path-integration system (hereafter referred to as *landmarks* and *path integration*, respectively, for brevity) could interact in two different ways: competition or integration. The cue-competition hypothesis assumes that one cue dominates navigation while the other cue is ignored (Shams, Kamitani, & Shimojo, 2000; Welch & Warren, 1980). In contrast, the cue-integration hypothesis proposes that the cues are integrated in a statistically optimal (Bayesian) fashion to reduce navigation variability (i.e., to achieve a more

consistent response; Cheng, Shettleworth, Huttenlocher, & Rieser, 2007; Shams & Beierholm, 2010). When two cues are optimally integrated, the response corresponds to the weighted average of the two cues, with the more reliable cue that yields less-variable responses having a greater weight (Ernst & Banks, 2002; Yuille & Bülthoff, 1996).

Do people optimally integrate their sense of direction and visual landmarks during navigation, or do they primarily rely on one cue at a time? The evidence seems mixed. Nardini, Jones, Bedford, and Braddick (2008) found that when both landmarks and path integration are present, response variability in a homing task is reduced, consistent with the cue-integration hypothesis. Other evidence in humans and animals supports the cue-competition hypothesis. Spatially shifted landmarks tend

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to dominate the homing direction (Foo, Warren, Duchon, & Tarr, 2005; Ratliff & Newcombe, 2008; Shettleworth & Sutton, 2005; Tcheang, Bühlhoff, & Burgess, 2011). When landmarks are shifted by more than 90°, landmark dominance often switches to path-integration dominance, an apparently nonlinear transition between two separate systems.

Cheng et al. (2007) proposed two principles to account for such mixed results. First, the subjective discrepancy between two cues determines whether they are integrated. Cues may be optimally integrated if they are not too discrepant, but they may compete if the discrepancy is subjectively large, consistent with contemporary work on “robust integration” (Girshick & Banks, 2009; Knill, 2007; Körding et al., 2007). Second, path integration is a special navigation system that functions as both a reference system (which detects and vetoes the discrepant cue) and a backup system (in case other cues fail). Therefore, cues are optimally integrated until a subjective conflict with the path-integration system is detected, whereupon path integration dominates. According to Bayesian integration, however, the less variable (i.e., more reliable) cue should dominate (Jacobs, 2002), so it remains unclear why path integration, which is typically more variable than landmark guidance (Nardini et al., 2008), would serve as a backup system.

The existing evidence for cue integration comes from measurements of response variability (e.g., the standard deviation of homing responses; Nardini et al., 2008), whereas the evidence for cue competition comes from measurements of response accuracy (e.g., mean homing direction relative to target direction; Foo et al., 2005). To determine whether landmarks and path integration are optimally integrated, one must measure both: Response variability to estimate the optimal weight for each cue and response accuracy to compute the actual reliance on each cue. In the present study, we measured both variables in the same paradigm to address three questions about cue interaction in human navigation. First, are landmarks and path integration optimally integrated to reduce homing variability? Second, when landmarks and path integration are in conflict, do they compete to determine the homing direction? Finally, do cue integration and competition govern different aspects of the response (i.e., variability and accuracy)?

To illustrate how variability and accuracy might behave differently, suppose you were an archer shooting at a target with a bow and arrow. Variability refers to how tightly clustered your arrows are, whereas accuracy refers to how close the cluster is to the bull's-eye. These two measures of performance are independent: The arrows may be tightly clustered (less variable) but miss the bull's-eye; conversely, they may be scattered all over the target (more variable), yet be quite accurate on average. A cardinal

rule of archery is to align one's stance perpendicularly to the shooting line. Now imagine that the target is surreptitiously moved—then where will you aim your arrows? If you rely solely on vision, your aim will shift along with the target. If you rely solely on your stance, you will continue shooting in the original direction—but blindly, so variability is likely to increase. If you optimally integrate vision and stance, your shots will be more consistent, but you will aim in between the new and old target locations, which will ensure that the arrow misses both marks. Thus, cue integration can actually reduce accuracy if a cue is biased, like the shifted target (Ernst & DiLuca, 2011). To avoid this outcome, you could aim at the visual target for accuracy but integrate vision and stance to reduce variability. In this solution, accuracy and variability obey different rules: A single cue dominates response direction, while cue integration reduces response variability.

We tested the cue-competition and cue-integration hypotheses using a homing task, in which participants faced a problem similar to an archer's in determining the response direction. Participants walked on a triangular path and were then asked to return to the home location they had visited during their walk (Fig. 1a). To investigate cue integration, we tested two single-cue conditions (path integration alone or landmarks alone) and one combined-cues condition (path integration and landmarks together). The cue-integration hypothesis predicts reduced variability in the combined-cues condition compared with the single-cue conditions. To investigate cue competition, we covertly shifted landmarks by 15° to 135° in six landmark-shift conditions. The cue-competition hypothesis predicts that a single cue will dominate the homing direction. The landmark-shift conditions also allowed us to examine whether conflicting cues are integrated to reduce variability. Finally, to manipulate the reliability of landmarks relative to path integration, we tested one group of participants with proximal landmarks (5.5 m away) and another group with distal landmarks (500 m away; Fig. 1b). The results show that cue integration and cue competition govern different aspects of the homing response: A single cue dominates homing direction, while both cues are near-optimally integrated to reduce homing variability.

Method

Participants

Eighteen people (7 female, 11 male; mean age = 25 years, $SD = 9$) participated in the experiment; 6 of them were tested with proximal landmarks and 12 with distal landmarks. Three additional participants tested with proximal landmarks either dropped out before finishing all five

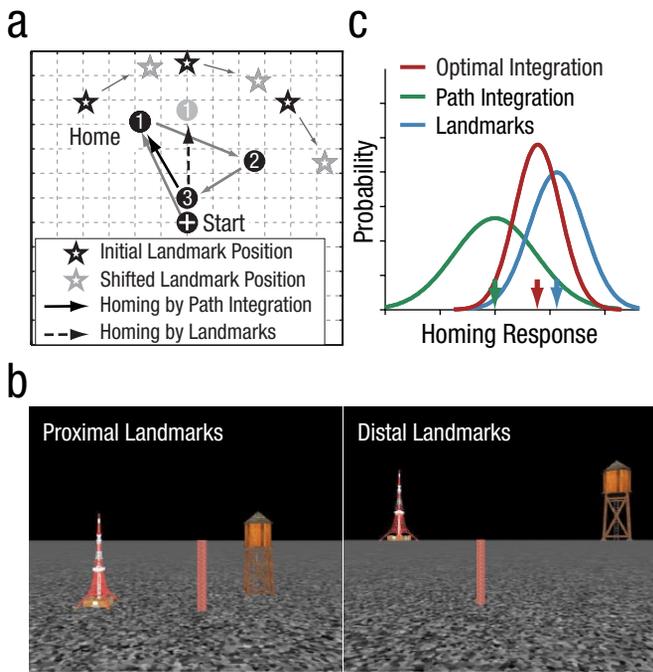


Fig. 1. Homing task and hypothetical homing responses. In the homing task (a), participants followed successive cues to walk from the starting location to Vertex 1 (home), Vertex 2, and Vertex 3 (the end of path), where they were then asked to return to the now-unmarked home location without assistance. When landmarks (represented here by stars) were shifted, homing could be based on path integration alone, landmarks alone, or their combination. Each square on the reference grid corresponds to 1 m². The views of the virtual environment from the start location (b) show the home pole with two proximal (left) or distal (right) landmarks. Hypothetical response probabilities based on path integration, landmarks, and the optimal integration of these two cues are shown in (c). Arrows indicate the mean homing direction, and the spread of distribution reflects variability.

sessions (2 participants) or were excluded because they responded randomly (1 participant). On the basis of prior research (Alais & Burr, 2004; Nardini et al., 2008), we planned to test 24 participants, but we stopped data collection after testing 21 because of difficulty in recruiting volunteers for the five-session experiment. We ended up with three similar-sized subgroups (see Results). All participants gave signed consent before the experiment.

Design

Participants performed a homing task by walking in a virtual environment (Figs. 1a and 1b). Specifically, guideposts cued them to walk on an unmarked path in the shape of a triangle: from the starting point to Vertex 1 (the home location), to Vertex 2, and then to Vertex 3 (the end of the path). They were then instructed to walk back to the remembered home location without the assistance of a guidepost. Participants were tested in nine conditions. In the path-integration-alone condition, no

landmarks were present during the trial, so participants had to rely solely on path integration for homing. In the landmarks-alone condition, fixed landmarks were present, but participants were disoriented at the end of the path before returning to the home location, so they had to rely solely on landmarks for homing. In the combined-cues condition, fixed landmarks were present, but participants were not disoriented. Additionally, there were six landmark-shift conditions: These were similar to the combined-cues condition, but landmarks were shifted about the end of the path before the homing response, while they were out of view. Six shift angles were tested: 15°, 30°, 45°, 90°, 115°, and 135°.

Virtual environment

The computer-generated virtual world was presented stereoscopically in a head-mounted display (Rockwell Collins, Cedar Rapids, IA; 63° horizontal × 53° vertical field of view, 1,280 × 1,024 pixels per eye, complete binocular overlap, 60-Hz frame rate). Head position was tracked with an inertial, ultrasonic tracking system (InterSense, Billerica, MA). Three towers were used as both proximal landmarks, which were placed 5.5 m from the end of the path (Vertex 3), and distal landmarks, which were placed 500 m away and scaled up to match the visual angle of proximal landmarks (Fig. 1b). Homing responses were expected to be less variable (i.e., more reliable) with proximal landmarks than distal landmarks because the former provide more precise positional information about the home location than the latter, given that they are much closer to home. The ground was textured with a gray Voronoi pattern, and the sky was black. Twenty triangular walking paths with different configurations were created; each path was presented twice, which yielded 40 trials per condition.

Procedure

Participants performed 40 homing trials in each of the nine conditions, with trials for each condition grouped together in the same block, for a total of 360 trials. On each trial, participants walked the path specified by four sequentially appearing poles (Fig. 1a). Each pole disappeared after the participant reached its location and the next pole appeared, so the full path was not visible simultaneously. Following Nardini et al. (2008), we asked participants to begin at the starting point facing the home pole, which provided a view of the home location relative to the landmarks (Fig. 1b). Participants were instructed to remember the home location, and then they walked three legs of the path to the end of the path (Vertex 3). A circular wall then surrounded the participant for 8 s. This wall had a radius of 5 m and a height of 6 m, and was

homogeneous in texture. During the time the circular wall appeared, the participant was either disoriented (in the landmarks-alone condition) or waited standing (all other conditions). The disorientation procedure was performed by an experimenter, who asked the participant to sit in a wheelchair at Vertex 3 and then rotated the wheelchair for 8 s (~73° per second). Participants then walked straight to where they remembered the home location to be, stopped, and pushed a response button. In landmark-shift conditions, all landmarks were covertly rotated en bloc, left or right around Vertex 3. The shift direction was randomly selected on each trial and was equally likely to be left or right in each condition. Landmark shifts always occurred out of the display's field of view as the participant walked from Vertex 2 to Vertex 3, which ensured that they were unable to see the shift. The initial view of home relative to the landmarks varied across trials.

Participants performed the experiment over five sessions (1.5 hr each). In the first two sessions, they completed the path-integration-alone, landmarks-alone, and combined-cues conditions, with one block of 20 trials in each condition per session. The order of conditions was counterbalanced. In the next three sessions, they performed the six landmark-shift conditions, two per session, in order of increasing shift angle, so the detection of large landmark shifts would not affect homing responses with small landmark shifts.

Data analysis

Response directions were standardized so that the correct homing direction was always at 0° ("north"), with positive values in the direction of landmark shift. Following prior navigation literature (e.g., Etienne & Jeffery, 2004; Knierim & Hamilton, 2011), we measured homing direction as the circular mean of response directions. Accordingly, the variability in homing was measured as the circular standard deviation of response direction. If path integration and landmarks are optimally integrated (Fig. 1c), then both mean homing direction (θ) and variance (σ^2) should be a weighted average of individual estimates, such that the weights assigned to landmarks (w_{LM}) and path integration (w_{PI}) are inversely proportional to their variability (Ernst & Banks, 2002; Yuille & Bülthoff, 1996):

$$\theta_{PI+LM} = w_{PI}\theta_{PI} + w_{LM}\theta_{LM}$$

$$\sigma_{PI+LM}^2 = \sigma_{PI}^2\sigma_{LM}^2 / (\sigma_{PI}^2 + \sigma_{LM}^2)$$

We used Murray and Morgenstern's (2010) method to derive optimal predictions for our circular data (see Supplementary Methods in the Supplemental Material available online for details).

Results

We first examined whether homing direction was influenced by the landmark shifts. While all participants in the proximal-landmark group consistently used landmarks when they shifted up to 90° (linear regressions of homing direction on landmark shift for each participant: all R^2 s > .99, ps < .001), participants tested with distal landmarks responded bimodally. Five participants followed distal landmarks up to a 90° shift (all R^2 s > .99, ps < .001), whereas the other 7 completely ignored distal landmarks (all R^2 s < .40, ps > .25). Because combining bimodal data would be misleading, we treated these two subgroups separately in subsequent analyses as the distal-landmark and distal-path-integration groups, respectively (individual data appear in Fig. S1 in the Supplemental Material).

Responses from a sample participant in each group are illustrated in Figure 2. Two response patterns are evident. First, participants consistently walked in the homing direction predicted either by landmarks (proximal- and distal-landmark groups) or by path integration (distal-path-integration group), but not somewhere in between. When landmarks shifted more than 90°, all participants switched to the path-integration direction. Second, homing responses were more consistent (i.e., less variable) when both path integration and landmarks were available than in the single-cue conditions—even with cue conflicts up to 90°. These observations are consistent with the earlier solution in the archery example of using a single cue to dominate response direction but using cue integration to reduce variability, and they were confirmed by the following statistical analyses.

Homing direction is consistent with cue competition

Homing direction is plotted as a function of landmark shift for each group in Figures 3a through 3c (individual-trial data appear in Fig. S3 in the Supplemental Material). Clearly, homing direction was dominated by one cue at a time rather than by a weighted average of the two. In the proximal-landmark group, homing direction followed the landmark prediction up to a 90° shift and was significantly different from the optimal-integration prediction at all shifts, all F s(1, 11) > 5.54, all ps < .05. The distal-landmark group showed the same pattern of responses, which differed significantly from the optimal-integration prediction for 15° to 90° shifts, all F s(1, 9) > 5.98, all ps < .05. In contrast, the distal-path-integration group's results were consistent with the path-integration prediction (Fig. 3c), which was again significantly different from the optimal-integration prediction for 15° to 115° shifts, all F s(1, 13) > 5.93, all ps < .05, and for 135° shifts, $F(1, 13) = 4.44$, $p = .057$.

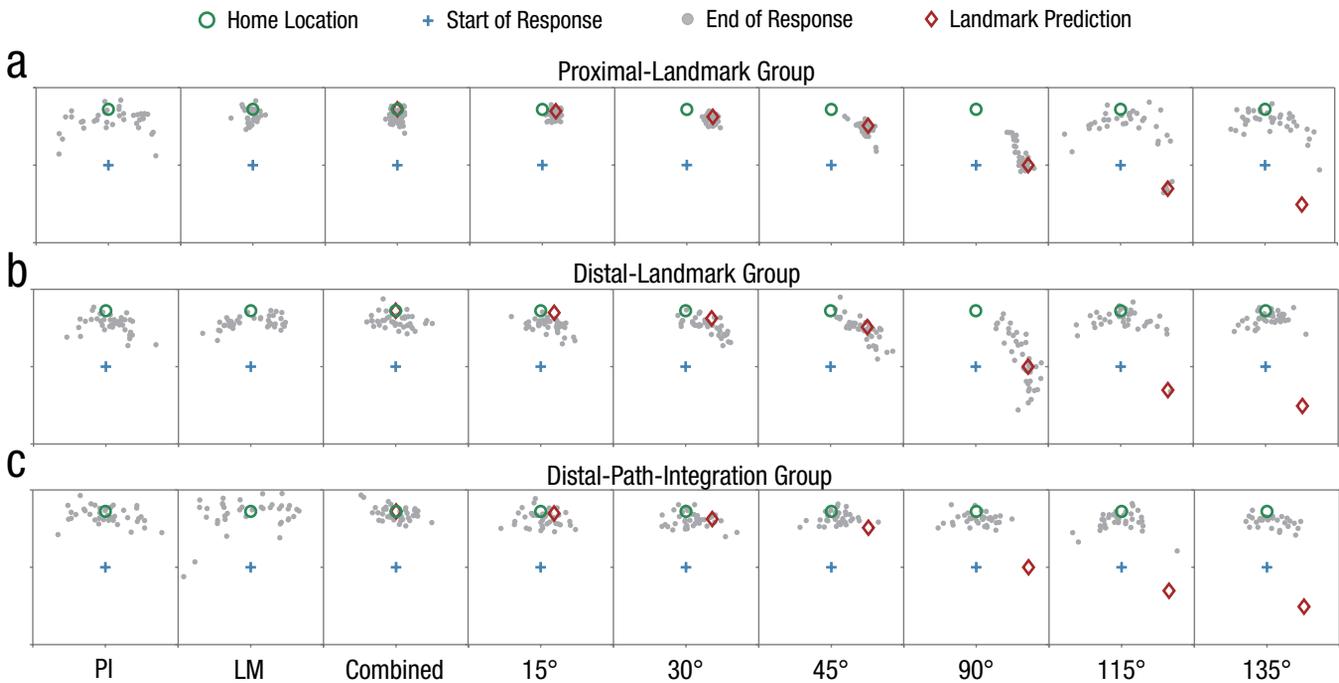


Fig. 2. Data from a sample participant in the (a) proximal-landmark, (b) distal-landmark, and (c) distal-path-integration group, separately for the nine conditions. Each box shows the start and end points of the participant’s 40 homing responses in that block, along with the actual home location, and the location predicted by landmarks. PI = path integration; LM = landmarks.

With large landmark shifts (115° and 135°), both landmark groups exhibited bimodal responses. A two-component cluster analysis confirmed that these consisted of one landmark-consistent component (all $F_s < 3.26$, $p_s > .12$, when observed homing direction was compared with the prediction based on landmarks) and one path-integration-consistent component (all $F_s < 1.33$, $p_s > .28$, when observed homing direction was compared with the path-integration prediction; see Supplementary Methods for details). Moreover, the bimodal pattern emerged around 115° as a nonlinear transition from responses that were landmark dominant to path-integration dominant. When landmarks shifted 115°, participants followed the landmarks on the first five trials, but most of them (7 of 11) switched to rely on path integration by the last five trials (see Fig. S3). These results suggest that the proximal- and distal-landmark groups relied solely on landmarks to determine their homing direction until landmarks were highly discrepant from path integration.

Surprisingly, landmarks dominated even when the cue conflict was theoretically detectable. We estimated the discrimination threshold of the path-integration system as $\sqrt{2}\sigma_{PI} = 47^\circ$ (Ernst & Banks, 2002), where σ_{PI} is the circular standard deviation of homing direction in the path-integration-alone condition. Similarly, the expected discrimination thresholds were 16° for proximal landmarks and 50° for distal landmarks. Yet we did not observe the switching point until 115°, which is more

than twice the discrimination thresholds. In other words, landmarks were not vetoed until they shifted by more than three times the path-integration system’s standard deviation ($M \pm 3\sigma_{PI} = \pm 99^\circ$).

Single-cue dominance was also observed in individual participants’ responses (Fig. 3d). Landmark shifts almost perfectly predicted the observed homing direction in both the proximal-landmark group ($R^2 = .99$), $t(31) = 4.81$, $p < .001$, and the distal-landmark group ($R^2 = .98$), $t(26) = 4.27$, $p < .001$, up to the observed switch (i.e., parsing out the path-integration-consistent component of the cluster analysis at 115° and 135°). Conversely, path integration predicted the homing responses in the distal-path-integration group and in the landmark group after the switch. Specifically, landmark shifts accounted for negligible variance in this data ($R^2 = .0002$), $t(59) = 0.18$, $p = .85$; instead, the mean homing direction (2.91° , $SE = 2.03$) was consistent with the path-integration prediction (1.44° , $SE = 0.40$), $F(1, 119) = 0.25$, $p = .62$. In sum, homing direction was consistent with the cue-competition hypothesis, both for group means and individual participants.

Homing variability is consistent with cue integration

In contrast, homing variability was consistent with the optimal-integration hypothesis—even when landmarks

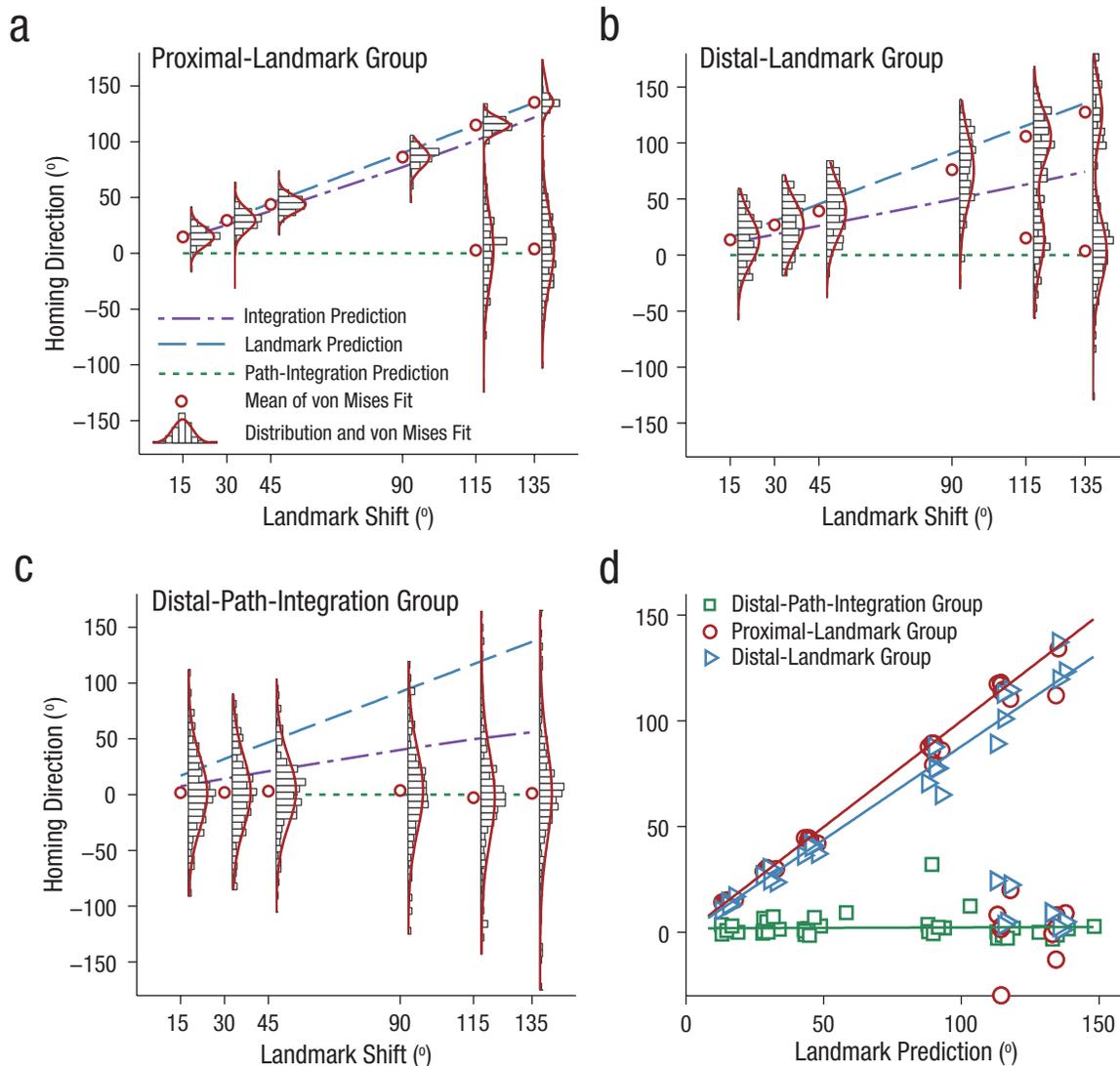


Fig. 3. Results for homing direction. The graphs in (a) through (c) show homing direction as a function of degrees of landmark shift, separately for the three groups (0° is the true home direction). Each graph shows predicted homing direction based on path integration, landmarks, and the optimal integration of these two cues, along with the observed distribution of homing directions in each condition (histograms), with von Mises fits to the corresponding circular distributions. The scatter plot (d) shows each participant's mean observed homing direction as a function of the predicted homing direction based on landmarks. Best-fitting regression lines are shown for each group.

were shifted up to 90° . Figure 4a shows that path integration and landmarks were optimally integrated to reduce variability in the combined-cues condition, compared with the single-cue conditions. For the proximal-landmark group, the mean standard deviation (10.11° , $SE = 1.11$) was similar to the optimal integration prediction (9.95° , $SE = 1.25$), $t(5) = 0.16$, $p = .88$, and was significantly lower than the mean standard deviation in the path-integration-alone condition (28.74° , $SE = 5.33$), $t(5) = 3.85$, $p = .01$. However, it was not significantly different from the standard deviation with landmarks alone (11.09° , $SE = 1.42$), $t(5) = 0.80$, $p = .46$, and thus might be

explained by landmark dominance. For the distal-landmark group, however, the observed standard deviation (22.87° , $SE = 1.27$) was close to the optimal integration prediction (22.15° , $SE = 1.27$), $t(4) = 0.61$, $p = .57$, and was significantly lower than that with either path integration alone (33.24° , $SE = 2.69$), $t(4) = 4.42$, $p = .01$, or landmarks alone (31.92° , $SE = 1.77$), $t(4) = 5.23$, $ps < .01$. Surprisingly, even the distal-path-integration group, which seemed to ignore the landmarks, benefited from optimal integration. Homing variability in the combined-cues condition (26.52° , $SE = 4.95$) was lower than that with either path integration alone (36.33° , $SE = 7.21$), $t(6) = 2.44$, $p = .05$,

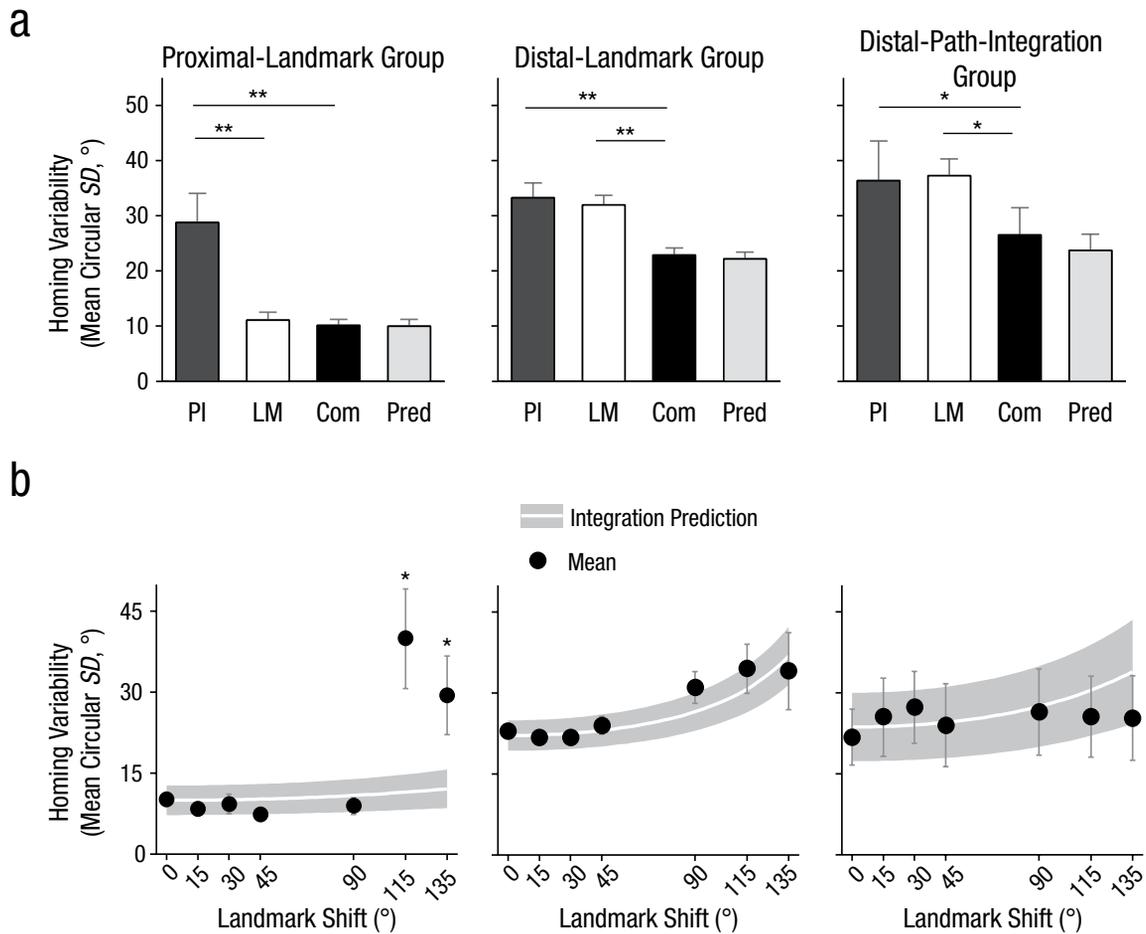


Fig. 4. Results for homing variability. The graphs in (a) show mean homing variability in the path-integration (PI), landmarks (LM), and combined-cues (Com) conditions, together with the predicted homing variability for the combined-cues condition (Pred), separately for the three groups. Error bars represent ± 1 SE. Asterisks indicate a significant difference between conditions ($*p \leq .05$, $**p < .01$). The graphs in (b) show mean homing variability in the landmark-shift conditions, together with the optimal-integration prediction (the white line represents the mean, and the gray band indicates the 95% confidence interval). An asterisk indicates a significant difference from the optimal-integration prediction ($*p \leq .05$). Error bars represent ± 1 SE.

or landmarks alone (37.27° , $SE = 3.03$), $t(6) = 3.45$, $p = .01$, and was no different from the optimal integration prediction (23.67° , $SE = 2.95$), $t(6) = 1.28$, $p = .25$.

Moreover, reduced variability was also observed when landmarks were shifted by as much as 90° (Fig. 4b). The observed mean standard deviations were consistent with the optimal integration predictions for all landmark shifts in all three groups (all $t_s < 2.03$, $p_s \geq .10$), except for the proximal-landmark group at 115° and 135° , $t_s(5) > 2.60$, $p_s < .05$. Note that one participant in the distal-path-integration group was excluded from this analysis because of unusually high variability (mean standard deviation: 53° , range: 28° – 75°).

The optimal-integration hypothesis also predicted the response variability within individual participants (Fig. 5). In the combined-cues condition, the optimal-integration hypothesis provided an excellent account of the within-subjects standard deviations ($R^2 = .89$), $F(1, 17) = 132.83$,

$p < .001$. In the landmark-shift conditions, the optimal-integration hypothesis remained a good predictor with shifts of 15° to 90° , accounting for 60% to 82% of the variance, all $F_s(1, 17) > 23.60$, $p_s < .001$. However, the optimal-integration hypothesis failed when landmarks were shifted by more than 90° , explaining only 3% and 18% of the variance at 115° and 135° , both $F_s(1, 17) < 3.65$, $p_s > .07$.

In addition, the optimal-integration hypothesis provided a significantly better account of these individual standard deviations than either path integration or landmarks alone. For landmark shifts up to 90° , linear regressions on the optimal-integration prediction ($R^2 = .73$, $SE = .05$, Fig. 5) were significantly better than those on the predictions based on landmarks ($R^2 = .48$, $SE = .05$) or path integration ($R^2 = .40$, $SE = .02$), all $t_s > 10.62$, $p < .005$. However, this was not the case with landmark shifts greater than 90° (115° and 135°), both $t_s < 1.42$, $p > .39$. In sum, these results indicate that path integration and

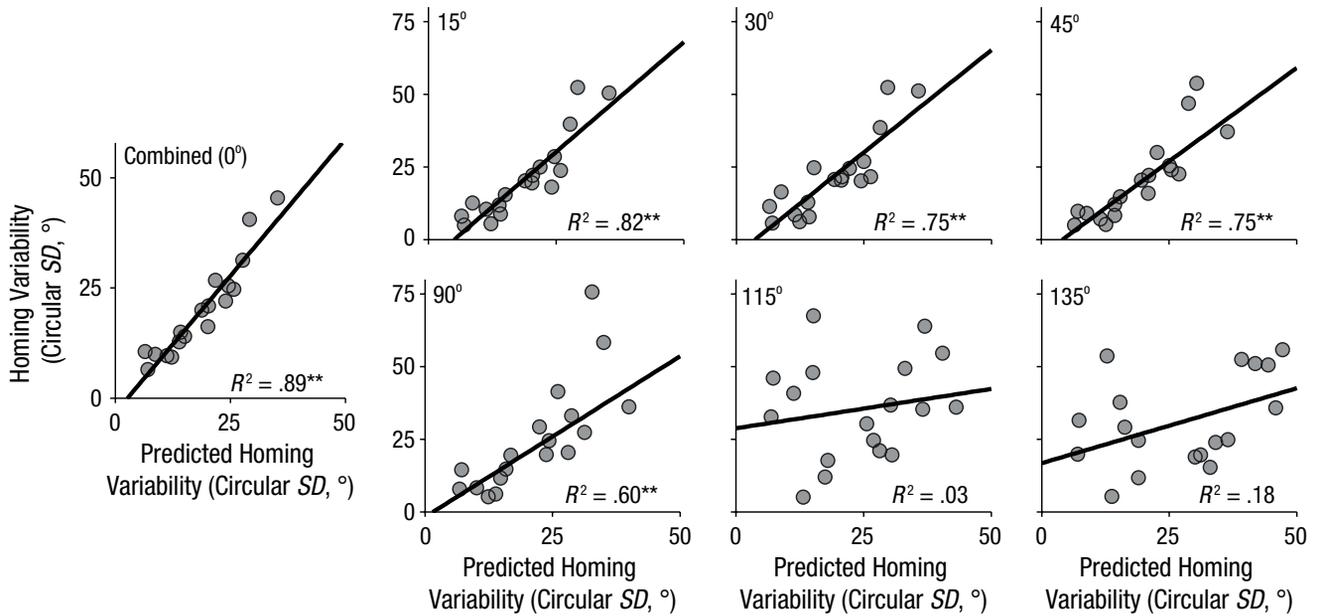


Fig. 5. Scatter plots (with best-fitting regression lines) showing mean observed homing variability in each landmark-shift condition as a function of homing variability predicted by the optimal-integration hypothesis. Asterisks indicate that the regression model explained a significant amount of the variance (** $p < .001$).

landmarks were near-optimally integrated to reduce response variability despite cue conflicts up to 90° , as measured at both the group and individual levels. The two cues appear to be integrated to reduce response variability until the discrepancy far exceeds the sensitivity of the path-integration system ($\geq 115^\circ$).

Discussion

We showed that accuracy and variability of homing responses obey different principles of cue interaction: Whereas landmarks and path integration are near-optimally integrated to reduce response variability, at the same time they compete to determine the homing direction. Neither cue-competition nor cue-integration theory predicts this combination of landmark dominance and optimal integration in homing responses (Cheng et al., 2007; Shams & Beierholm, 2010; Yuille & Bühlhoff, 1996). Yet the results are remarkably consistent with the observation that landmarks reset the orientation, but not the precision, of the path-integration system in animals (Etienne & Jeffery, 2004; Etienne, Maurer, Boulens, Levy, & Rowe, 2004; Knierim, Kudrimoti, & McNaughton, 1998).

Our study helps to explain prior mixed results for cue interaction in navigation: Previous studies measured either accuracy or variability, but not both. Consistent with the cue-integration hypothesis, our results showed that landmarks and path integration are optimally integrated to reduce variability, even with marked cue conflicts. Consistent with the cue-competition hypothesis, our

findings revealed that homing direction is determined by one cue at a time rather than by their combination. Landmarks generally dominate with moderate cue conflicts, whereas path integration dominates with large conflicts. Our participants switched from proximal landmarks to less-reliable path integration at about 115° , which suggests that the more reliable cue does not always dominate.

To account for such nonlinear interactions between conflicting cues in human perception, models of robust cue integration modify assumptions about either the prior probability distribution or the likelihood function for individual cues (Girshick & Banks, 2009; Knill, 2007). It has been proposed that robust-integration or causal-inference models apply to cue interactions in animal navigation (Cheng et al., 2007; Shams & Beierholm, 2010). However, these models have difficulty explaining the dissociation of accuracy and variability observed here, because they assume that these properties should obey the same integration rule. To explain our results, additional assumptions would have to be invoked.

The simultaneous cue dominance and cue integration we observed is consistent with the hypothesis that landmarks reset the orientation, but not the precision, of the path-integration system. Path integration is known to accumulate error in the homing estimate over time (e.g., uncertainty in the “homing vector” from one’s current position to the estimated home location), independent of the error associated with visual landmarks. Thus, landmarks could be used to reset the direction of the homing vector without

affecting the variability of the homing estimate. This resetting hypothesis is consistent with current neurophysiological models of navigation (Knierim & Hamilton, 2011; Yoder, Clark, & Taube, 2011). Specifically, shifted landmarks reset the directional tuning of place cells, head-direction cells, and grid cells, but do not significantly affect their receptive field size, tuning-curve width, or spacing properties (Hafting, Fyhn, Molden, Moser, & Edvard, 2005; Knierim et al., 1998; Taube, Muller, & Ranck, 1990; see also Brandon et al., 2011). Thus, shifted landmarks could dominate the homing direction while still being integrated with path integration to reduce variability.

This resetting account suggests that integration and competition may occur during different stages of the homing task. On the outbound path, fixed landmarks are integrated with path integration to form a more precise (i.e., less variable) homing estimate. When the navigator turns onto the homebound path, visible landmarks (shifted or not) reset the direction of the homing vector but leave its precision unchanged; cue integration then continues on the homebound path. Thus, cue integration reduces variability in the homing estimate over the entire path, whereas cue competition determines the homing direction at the response stage. But if landmark shifts are detected (e.g., exceeding 3 standard deviations of the path-integration system), the navigator switches from landmark guidance to path integration, with no further cue integration. Consistent with this interpretation, previous findings have shown that landmarks available on the outbound path reduce the variability of path integration (Philbeck & O'Leary, 2005), whereas modified landmarks on the response path dominate the homing direction (Foo et al., 2005; Tcheang et al., 2011).

Why might landmarks dominate with moderate cue conflicts, while less-reliable path integration dominates with large conflicts? Cheng et al. (2007) attributed to path integration the privileged status of a reference system that detects landmark discrepancies and a backup system if landmark guidance fails. This solution seems well-adapted to environments with potentially unstable landmarks that might move, change, or disappear, such as a loose rock or rotting log. A subjectively discrepant landmark would be rejected, and path integration would take over (e.g., Wehner, Michel, & Antonsen, 1996). However, the reference-system hypothesis is at odds with the resetting hypothesis, for the same system cannot simultaneously reject discrepant landmarks and be reset by them. Our finding that path integration tolerates large cue conflicts that are theoretically detectable favors the resetting account, with a possible role for path integration as a very weak reference system. Indeed, this permissiveness actually facilitates cue integration and the dominance of landmarks over a wide range of cue discrepancies.

In other environmental contexts, it may not be adaptive for path integration to have a privileged status. In

environments with stable landmarks that uniquely specify the home location, such as distinctive trees, rock outcrops, or streams in a meadow (or their configurations), we would expect landmarks to dominate. Conversely, in environments with ambiguous features, such as highly unstable landmarks or confusable trees in a forest, we would expect path integration to dominate—despite being normally less reliable. Thus, we speculate that dominance may depend more on cue specificity than on cue reliability or a privileged status. Cue specificity in different environmental contexts might be treated as an ecological constraint on navigation or a Bayesian prior (see Cheng et al., 2007; Shams & Beierholm, 2010, for discussion). These intuitions require a more formal theoretical development.

We conclude that visual landmarks and path integration interact to guide human navigation. The two cues are near-optimally integrated to reduce response variability but compete nonlinearly to dominate the response direction. These findings bear a striking similarity to behavioral and neurophysiological results in nonhuman animal navigation, which suggests that analogous solutions may be preserved across a variety of species.

Author Contributions

M. Zhao and W. H. Warren designed the experiment and wrote the manuscript. M. Zhao conducted the experiment and analyzed the data. Both authors approved the final version of the manuscript for submission.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information can be found at <http://pss.sagepub.com/content/by/supplemental-data>

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