

Running head: Cue Interaction in Human Navigation

How You Get There From Here:

Interaction of Visual Landmarks and Path Integration in Human Navigation

Mintao Zhao and William H. Warren

Department of Cognitive, Linguistic, & Psychological Sciences

Brown University

Please address correspondence to MZ or WHW.

Department of Cognitive, Linguistic, & Psychological Sciences

Brown University

Providence, RI 02912.

Email: bill_warren@brown.edu.

MZ is now at Max Planck Institute for Biological Cybernetics, 72076 Tübingen, Germany (email: mintao.zhao@tuebingen.mpg.de).

Word count: 2010 (Intro, Discussion, and Acknowledgement); 2240 (Method and Results)

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

ABSTRACT

How do people combine their sense of direction with visual landmarks during navigation? Cue integration theory predicts 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 path integration and landmarks. We find that the two cues are near-optimally integrated to reduce variability, even when landmarks are shifted up to 90°. Yet the homing direction is dominated by a single cue, which switches from landmarks to path integration with landmark shifts >90°. These findings suggest that integration and 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, implying 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

Humans share two fundamental navigation mechanisms with other animals. One is path integration (PI), the “sense of direction” that keeps track of one’s position and orientation based primarily on self-motion information (Etienne & Jeffery, 2004; Kearns, Warren, Duchon, & Tarr, 2002; Loomis et al., 1993). Another is landmark guidance, which relies on visual landmarks and other environmental cues for homing, reorientation, and wayfinding (Collett, 2010; Trullier, Wiener, Berthoz, & Meyer, 1997). Theoretically, these two systems could interact in two different ways: competition or integration. The 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 primarily rely on one system at a time? The results seem mixed. Nardini, Jones, Bedford, and Braddick (2008) found that when both landmarks and PI are present, response variability in a homing task is reduced, consistent with the integration hypothesis. Other evidence in humans and animals supports the competition hypothesis. Spatially shifted landmarks tend to dominate the homing direction (Foo, Warren, Duchon, & Tarr, 2005; Ratliff & Newcombe, 2008; Shettleworth & Sutton, 2005; Tcheang, Bülthoff, & Burgess, 2011). When

landmarks are shifted by more than 90°, landmark-dominance often switches to PI-dominance, an apparently non-linear 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 compete if the discrepancy is subjectively large, consistent with contemporary work on “robust integration” (Girshick & Banks, 2009; Körding et al., 2007; Knill, 2007). Second, PI is a special navigation system that functions as both a reference system (which detects and vetoes the discrepant cue) and a back-up system (in case other cues fail). Therefore cues are optimally integrated until a subjective conflict with the PI system is detected, whereupon PI dominates. According to Bayesian integration, however, the less variable (i.e., more reliable) cue should dominate (Jacobs, 2002), so it remains unclear why PI, which is typically more variable than landmarks (Nardini et al., 2008), would serve as a back-up 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 PI are optimally integrated, both must be measured: 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 PI optimally

integrated to reduce homing variability? Second, when landmarks and PI are in conflict, do they compete to determine the homing direction? Finally, do integration and competition govern different aspects of the response (i.e. variability and accuracy)?

To illustrate how variability and accuracy might behave differently, consider an archer shooting at a target. *Variability* refers to how tightly clustered her 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 perpendicular to the shooting line. Now imagine that the target is surreptitiously moved – then where will the archer aim her arrows? If she relies solely on vision, her aim will shift along with the target. If she relies solely on her stance, she will continue shooting in the original direction – but blindly, so variability is likely to increase. If she optimally integrates vision and stance, her shots will be more consistent, but she will aim in between the new and old target locations, insuring 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, the archer could aim at the visual target for accuracy, but integrate vision and stance to reduce variability. On 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 integration hypotheses using a homing task (**Figure 1a**), in which participants faced a problem similar to the archer's in determining the response

direction. Participants walked on a triangular path and then returned to the “home” location. To investigate cue integration, we tested two *single-cue conditions* (PI alone or landmarks alone) and one *combined condition* (PI + landmarks). The integration hypothesis predicts reduced variability in the combined condition compared to the single-cue conditions. To investigate cue competition, we covertly shifted landmarks by 15° to 135° in six *landmark shift conditions*. The competition hypothesis predicts that a single cue will dominate the homing direction. The shift conditions also allowed us to examine whether conflicting cues are integrated to reduce variability. Finally, to manipulate the reliability of landmarks relative to PI, we tested one group of participants with proximal landmarks (5.5m away) and another group with distal landmarks (500m away) (**Figure 1b**). The results show that cue integration and cue competition govern different aspects of the homing response: a single cue dominates homing direction, while at the same time both cues are near-optimally integrated to reduce homing variability.

METHODS

Participants. Eighteen people (seven female; mean age = 25, SD = 9) participated in the experiment, six of them were tested with proximal landmarks and twelve with distal landmarks. Three additional participants tested with proximal landmarks either dropped out before finishing all five sessions (two participants) or were excluded because they responded randomly (one participant). Based on prior research (Alais & Burr, 2004; Nardini et al., 2008), we planned to test twenty-four participants, but we stopped data collection after testing twenty-one due to difficulty in recruiting volunteers for the five-session experiment. To anticipate, we

ended up with three similar-sized subgroups (see Results). All participants gave signed consent before the experiment.

Design. Participants performed a triangle completion task in an ambulatory virtual environment (**Figure 1a**). Specifically, they walked on a triangular path (from Start to Vertex 3, the response point), and were then instructed to walk back to the remembered Home location (Vertex 1). Nine conditions were tested: (1) *PI alone*: no landmarks present during the trial, participants had to rely solely on PI for homing; (2) *Landmarks alone*: fixed landmarks present, but participants were disoriented at the response point before homing, so they had to rely solely on landmarks for homing; (3) *Combined condition*: fixed landmarks present, no disorientation; and (4-9) *Conflict conditions*: same as combined condition, but landmarks were shifted about the response point 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 (HMD, Rockwell Collins, IA; 63° H × 53° V field of view, 1024×768 pixels per eye, 60 Hz frame rate). Head position was tracked with an inertial/ultrasonic tracking system (InterSense, MA). Three towers were used as both *Proximal* landmarks, which were placed 5.5 m from the response point (Vertex 3), and *Distal* landmarks, which were placed 500 m away and scaled up to match the visual angle of proximal landmarks (**Figure 1b**). Homing responses were expected to be less variable (i.e., more reliable) with proximal landmarks than distal landmarks because they 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, yielding 40 trials per condition.

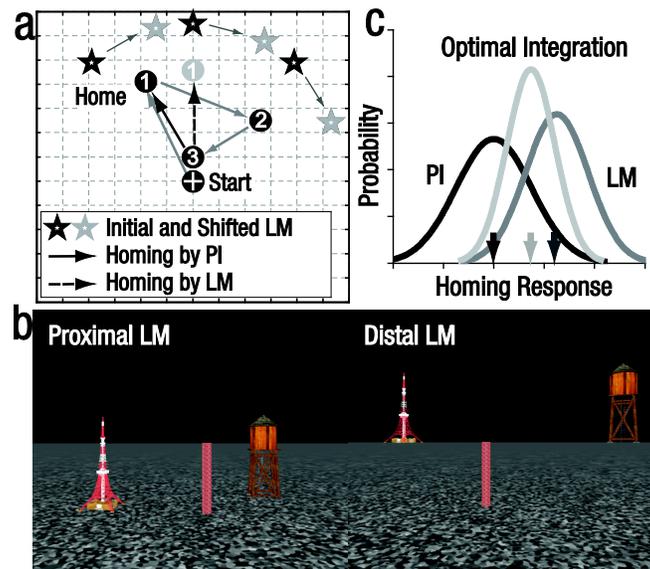


Figure 1

Procedure. Participants performed 40 homing trials in each of the nine conditions, with trials blocked by condition, for a total of 360 trials. On each trial, participants walked the path specified by four sequentially appearing poles (**Figure 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), participants began at the start point facing the Home pole, providing a view of the Home location relative to the landmarks (**Figure 1b**). Participants were instructed to remember the Home location, and then walked three legs of the path to the response point (Vertex 3). A cylindrical wall appeared for 8 s (radius 5 m, height 6 m, homogeneous texture, centered on the response point); during this time, the participant was

either disorientated (passive rotation in a wheelchair at $\sim 73^\circ/s$ for 8 s, landmarks alone condition) or waited standing (all other conditions). Participants then walked straight to the remembered home location, stopped, and pushed a response button. In landmark shift conditions, all landmarks were covertly rotated en bloc, left or right about the response point. The shift direction was randomly selected on each trial, and equated left/right in each condition. Landmark shifts always occurred out of the HMD's field of view as the participant walked from Vertex 2 to 3, insuring that they were unable to see the shift. The initial locations of the landmarks were identical across trials.

Participants performed the experiment over five sessions (1.5 hours each). In the first two sessions, they completed the PI, landmark, and combined conditions, with one block of 20 trials in each condition per session, counterbalanced for order. In the next three sessions, they performed the six shift conditions, two per session, in increasing order, so the conflict would not be revealed prior to subjective detection.

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. Consistent with prior navigation literature (e.g., Etienne & Jeffery, 2004; Knierim & Hamilton, 2011), homing direction was measured as the circular mean of response directions. Accordingly, the variability in homing was measured as the circular standard deviation (circular SD) of response direction. If PI and landmarks are optimally integrated (**Figure 1c**, gray line), 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 PI (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 online supplementary methods for details).

RESULTS

We first examined whether homing direction was influenced by the landmark shifts. While all participants in the *Proximal LM* group consistently followed the landmarks up to a 90° shift (linear regressions of homing direction on landmark shift for each participant: all $R^2 > 0.99$, $P < 0.001$), participants tested with distal landmarks responded bimodally. Five participants followed distal landmarks up to a 90° shift (all $R^2 > 0.99$, $P < 0.001$), whereas the other seven completely ignored distal landmarks (all $R^2 < 0.40$, $P > 0.25$). Because combining bimodal data would be misleading, we treated these two subgroups separately in subsequent analyses as the *Distal LM* and *Distal PI* groups, respectively (Individual data appear in online supplementary **Figure S1**)

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

either predicted by landmarks (Proximal and Distal LM groups) or by PI (Distal PI group), but not somewhere in between. When landmark shifts exceeded 90°, all participants switched to the PI direction. Second, homing responses were more consistent (i.e., less variable) when both PI and landmarks were available than in the single-cue conditions – even with cue conflicts up to 90°. These observations are consistent with the archer’s solution of a single cue dominating response direction but cue integration reducing variability, and are confirmed by the following statistical analyses.

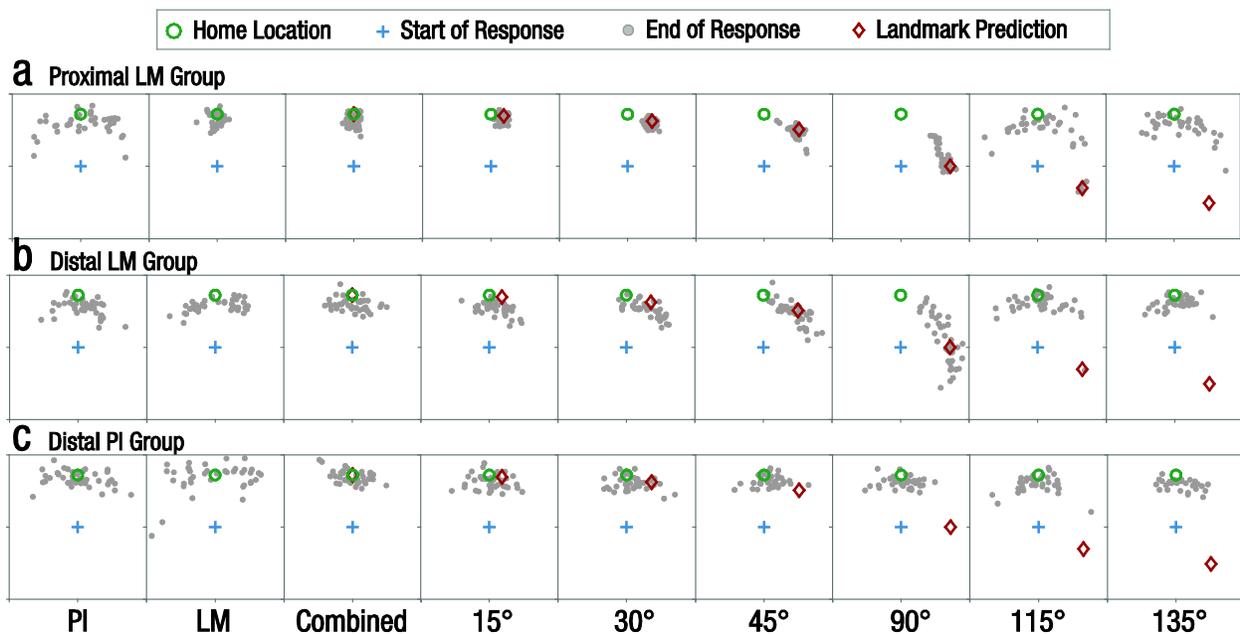


Figure 2

Homing direction is consistent with cue competition

Homing direction is plotted as a function of landmark shift for each group in **Figure 3a-c**, with the observed data indicated by histograms (individual trial data appear in on-line supporting **Figure S3**). The predictions of the cue dominance hypothesis (PI or LM) and cue

integration hypothesis are represented by dashed lines. Clearly, homing direction was dominated by one cue at a time rather than by a weighted average of the two. In the Proximal LM group (**Figure 3a**), homing direction followed the landmark prediction up to a 90° shift, and was significantly different from the optimal integration prediction at all shifts (all $F_{1,11} > 5.54$, all $P < 0.05$). The Distal LM group showed the same pattern of responses (**Figure 3b**), differing significantly from the integration prediction for 15° to 90° shifts (all $F_{1,9} > 5.98$, all $P < 0.05$). In contrast, the Distal PI group was consistent with the PI prediction (**Figure 3c**), again significantly different from the integration prediction for 15° to 115° shifts (all $F_{1,13} > 5.93$, all $P < 0.05$; for 135° shift, $F_{1,13} = 4.44$, $P = 0.057$).

With large landmark shifts (115° and 135°), both LM groups exhibited bimodal responses (**Figure 3a-b**). A two-component cluster analysis confirmed that these consisted of one landmark-consistent component (all $F < 3.26$, $P > .12$, when observed homing direction was compared to landmark prediction) and one PI-consistent component (all $F < 1.33$, $P > .28$, when observed homing direction was compared to PI prediction) (see online supplementary methods for details). Moreover, the bimodal pattern emerged around 115° as a nonlinear transition from landmark-dominant to PI-dominant responses. In the 115° shift condition, participants followed the landmarks on the first five trials, but most of them (7 of 11) switched to rely on PI by the last five trials (see online supplementary **Figure S3**). These results suggest that the Proximal and Distal LM groups relied solely on landmarks to determine their homing direction until the landmarks were highly discrepant from PI.

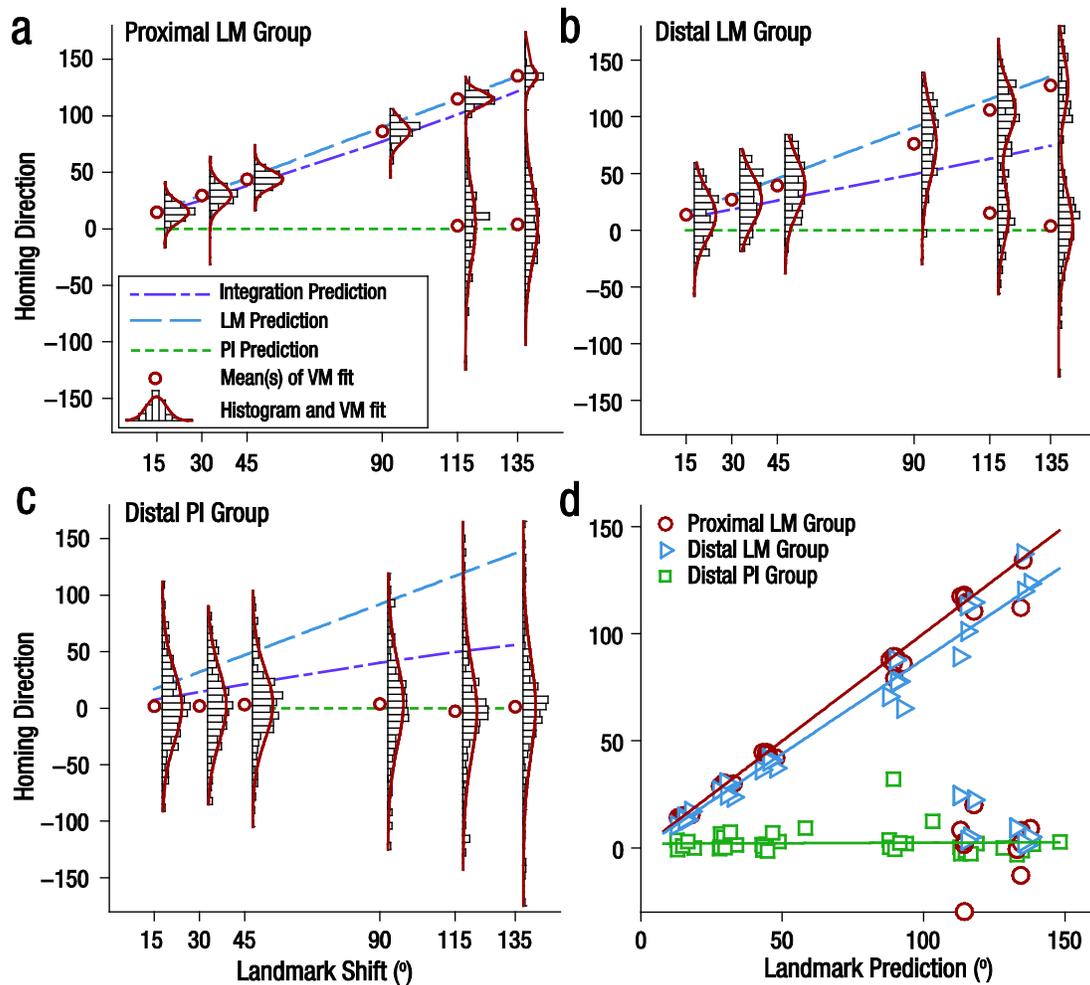


Figure 3

Surprisingly, landmarks dominated even when the cue conflict was theoretically detectable. We estimated the discrimination threshold of the PI system as $\sqrt{2}\sigma_{PI} = 47^\circ$ (Ernst and Banks, 2002), where σ_{PI} is the circular SD of homing direction in the PI-only condition. Similarly, the expected discrimination thresholds are 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 PI system's standard deviation ($M \pm 3\sigma_{PI} = \pm 99^\circ$).

Single-cue dominance was also observed in individual participants' responses (**Figure 3d**). Landmark shifts almost perfectly predict the observed homing direction in both the Proximal LM group (red line, $R^2 = 0.99$, $t_{31} = 4.81$, $P < 0.001$) and the Distal LM group (blue line, $R^2 = 0.98$, $t_{26} = 4.27$, $P < 0.001$) up to the observed switch (i.e. parsing out the PI-consistent component of the cluster analysis at 115° and 135°). Conversely, path integration predicts the homing responses in the Distal PI group, and in the LM group after the switch (green line). Specifically, landmark shifts account for negligible variance in this data ($R^2 = 0.0002$, $t_{59} = 0.18$, $P = 0.85$); instead, the mean homing direction (\pm SE) is consistent with the PI prediction ($2.91 \pm 2.03^\circ$ vs. $1.44 \pm 0.40^\circ$, $F_{1,119} = 0.25$, $P = 0.62$). In sum, the results indicate that homing direction is 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 were shifted up to 90° . **Figure 4a** shows that PI and landmarks were optimally integrated to reduce variability in the combined condition, compared to the single-cue conditions. For the Proximal LM group (left), the mean SD was similar to the optimal integration prediction ($10.11 \pm 1.11^\circ$ vs. $9.95 \pm 1.25^\circ$, $t_5 = 0.16$, $P = 0.88$), and was significantly lower than that with PI alone ($28.74 \pm 5.33^\circ$, $t_5 = 3.85$, $P = 0.01$). However, it was not different from the SD with landmarks alone ($11.09 \pm 1.42^\circ$, $t_5 = 0.80$, $P = 0.46$), and thus might be explained by landmark dominance. For the Distal LM group (center), however, the observed SD was close to the optimal integration prediction ($22.87 \pm 1.27^\circ$ vs. $22.15 \pm 1.27^\circ$, $t_4 = 0.61$, $P = 0.57$), and was

significantly lower than that with either PI alone ($33.24 \pm 2.69^\circ$, $t_4 = 4.42$, $P = 0.01$) or landmarks alone ($31.92 \pm 1.77^\circ$, $t_4 = 5.23$, $P_s < 0.01$). Surprisingly, even the Distal PI group (right), which seemed to ignore the landmarks, benefited from optimal integration. Homing variability in the combined condition ($26.52 \pm 4.95^\circ$) was lower than that with either PI alone ($36.33 \pm 7.21^\circ$, $t_6 = 2.44$, $P = 0.05$) or landmarks alone ($37.27 \pm 3.03^\circ$, $t_6 = 3.45$, $P = 0.01$), and was no different from the optimal integration prediction ($23.67 \pm 2.95^\circ$, $t_6 = 1.28$, $P = 0.25$).

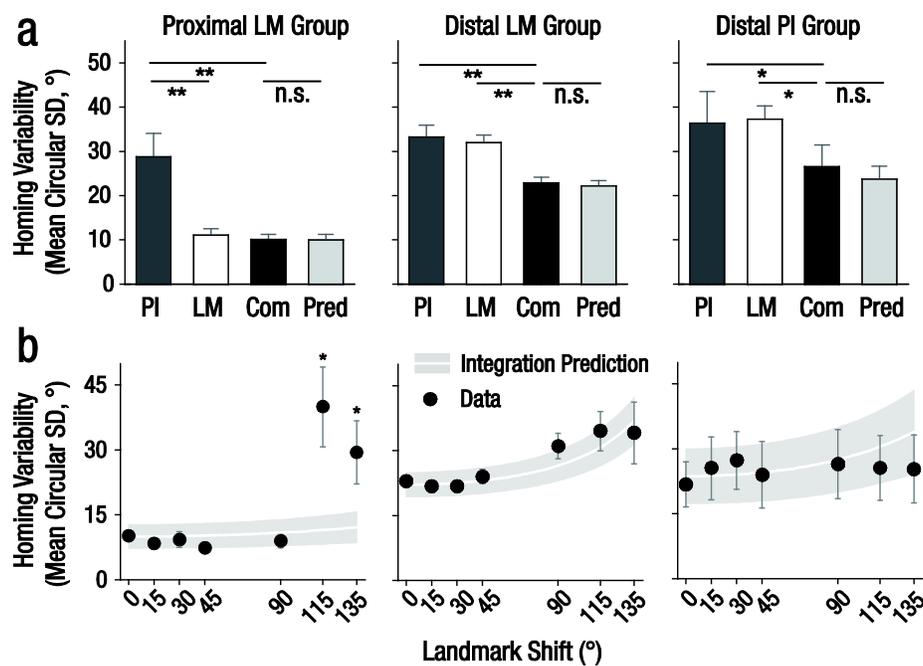


Figure 4

Moreover, reduced variability was also observed when PI and landmarks conflicted by as much as 90° (Figure 4b). The observed mean SDs were consistent with the optimal integration predictions for all landmark shifts in all three groups (all $t < 2.03$, $P \geq 0.10$), except the Proximal LM group at 115° and 135° ($t_{5s} > 2.60$, $P_s < 0.05$).

The optimal integration hypothesis also predicted the response variability within individual participants (**Figure 5**). In the combined condition, the integration hypothesis provided an excellent account of the within-subject SDs ($R^2 = 0.89$; $F_{1,17} = 132.83$, $P < 0.001$). In the landmark shift conditions, the integration hypothesis remained a good predictor with shifts of 15° to 90° , accounting for 60% to 82% of the variance (all $F_{1,17} > 23.60$, $P < 0.001$). However, optimal integration fell apart when landmarks were shifted by more than 90° , explaining only 3% and 18% of the variance at 115° and 135° (both $F_{1,17} < 3.65$, $P > 0.07$).

In addition, optimal integration provided a significantly better account of these individual SDs than either PI or landmarks alone. For landmark shifts up to 90° , linear regressions on the optimal prediction (R^2 values of 0.73 ± 0.05 , **Figure 5**) were significantly better than those on the landmark prediction (0.48 ± 0.05) or the PI prediction (0.40 ± 0.02) (all $t_s > 10.62$ $P < 0.005$). However, this was not the case with landmark shifts greater than 90° (115° and 135° , both $t_s < 1.42$, $P > 0.39$). In sum, these results indicate that PI and 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 PI system ($\geq 115^\circ$).

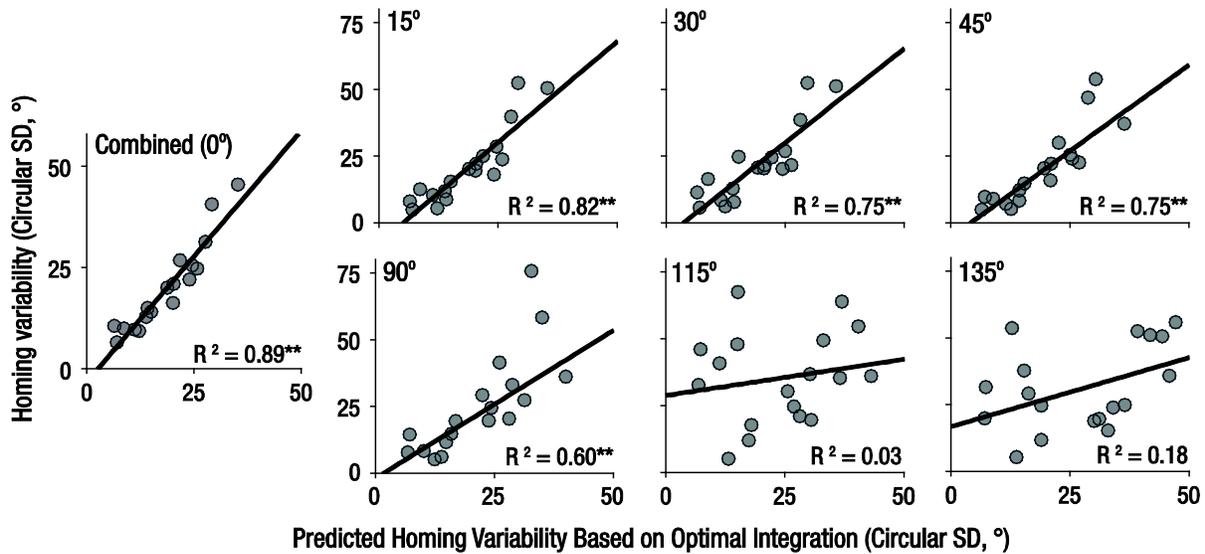


Figure 5

DISCUSSION

We show that accuracy and variability of homing responses obey different principles of cue interaction: whereas landmarks and PI 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 PI system in animals (Etienne & Jeffery, 2004; Etienne, Maurer, Boulens, Levy, & Rowe, 2004; Knierim et al., 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, we find that landmarks and path integration are optimally integrated to reduce variability, even with marked cue conflicts. Consistent with the cue competition hypothesis, homing direction is determined by one cue at a time rather than their combination. Landmarks generally dominate with moderate cue conflicts, whereas PI dominates with large conflicts. Our participants switched from proximal LM to *less-reliable* PI at about 115°, suggesting 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 serve to reset the orientation, but not the precision, of the PI system. PI 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 et al., 2005; Knierim et al., 1998; Taube et al., 1990; see also Brandon et al., 2011). Thus, shifted landmarks could dominate the homing direction while still being integrated with PI 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 PI 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 three standard deviations of the PI system), the navigator switches to PI, with no further cue integration. Consistent with this interpretation, landmarks available on the outbound path have been shown to reduce the variability of PI (Philbeck & O'Leary, 2005), whereas modified landmarks on the response path dominate the homing direction (Foo et al., 2005; Tcheang, Bühlhoff & Burgess, 2011).

Why might landmarks dominate with moderate cue conflicts, while less-reliable PI dominates with large conflicts? Cheng, et al. (2007) attributed to PI the privileged status of a

reference system that detects landmark discrepancies, and a back-up system if landmarks fail. 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 PI 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 PI tolerates large cue conflicts that are theoretically detectable favors the resetting account, with a possible role for PI as a very weak reference system. Indeed, this permissiveness actually serves to facilitate cue integration and landmark dominance over a wide range of cue discrepancies.

In other environmental contexts, it may not be adaptive for PI 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 (*spatial aliasing*), we would expect PI 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 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 non-human animal navigation, suggesting that analogous solutions may be preserved across a variety of species.

Author Contributions

MZ and WHW designed the experiment and wrote the paper. MZ conducted the experiment and analyzed the data. Both authors approved the final version of the manuscript for submission.

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.

Acknowledgements

This study was supported by NSF Grant BSC-0843940 to WHW. We thank Nora Newcombe, Marco Nardini, Martin Banks, Frances Wang, Weimin Mou, and three anonymous reviewers for their very helpful comments.

REFERENCES

- Alais, D., & Burr, D. (2004). The ventriloquist effect results from near-optimal bimodal integration. *Current Biology, 14*, 257-262.
- Brandon, M. P., Bogaard, A. R., Libby, C. P., Connerney, M. A., Gupta, K., & Hasselmo, M. E. (2011). Reduction of theta rhythm dissociates grid cell spatial periodicity from directional tuning. *Science, 332*, 595-599.
- Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. J. (2007). Bayesian integration of spatial information. *Psychological Bulletin, 133*, 625-637.
- Collett, M. (2010). How desert ants use a visual landmark for guidance along a habitual route. *Proceedings of the National Academy of Sciences of the USA, 107*, 11638-11643.
- Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature, 415*, 429-433.
- Ernst, M. O., & DiLuca, M. (2011). Multisensory perception: from integration to remapping. In J. Trommershauser, K. P. Kording & M. S. Landy (Eds.), *Sensory cue integration* (pp. 224-250). New York: Oxford University Press.
- Etienne, A. S., & Jeffery, K. J. (2004). Path integration in mammals. *Hippocampus, 14*, 180-192.
- Etienne, A. S., Maurer, R., Boulens, V., Levy, A., & Rowe, T. (2004). Resetting the path integrator: a basic condition for route-based navigation. *Journal of Experimental Biology, 207*, 1491-1508.

- Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map- versus landmark-based navigation of novel shortcuts. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 31, 195-215.
- Girshick, A. R., & Banks, M. S. (2009). Probabilistic combination of slant information: Weighted averaging and robustness as optimal percepts. *Journal of Vision*, 9(9:8), 1-20. doi: 10.1167/9.9.8
- Hafting, T., Fyhn, M., Molden, S., Moser, M.-B., & Edvard I, M. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature*, 436, 801-806.
- Jacobs, R. A. (2002). What determines visual cue reliability? *Trends in Cognitive Sciences*, 6, 345-350.
- Kearns, M. J., Warren, W. H., Duchon, A. P., & Tarr, M. J. (2002). Path integration from optic flow and body senses in a homing task. *Perception*, 31, 349-374.
- Knierim, J. J., & Hamilton, D. A. (2011). Framing spatial cognition: Neural representations of proximal and distal frames of reference and their roles in navigation. *Physiological Reviews*, 91, 1245-1279.
- Knierim, J. J., Kudrimoti, H. S., & McNaughton, B. L. (1998). Interactions between idiothetic cues and external landmarks in the control of place cells and head direction cells. *Journal of Neurophysiology*, 80, 425-446.
- Knill, D. C. (2007). Robust cue integration: A Bayesian model and evidence from cue-conflict studies with stereoscopic and figure cues to slant. *Journal of Vision*, 7(7:5), 1-24. doi 10.1167/7.7.5

- Körding, K. P., Beierholm, U., Ma, W. J., Quartz, S., Tenenbaum, J. B., & Shams, L. (2007). Causal inference in multisensory perception. *PLoS One*, 2(9), e943. Doi: 10.1371/journal.pone.0000943
- Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., Pellegrino, J. W., & Fry, P. A. (1993). Nonvisual navigation by blind and sighted: Assessment of path integration ability. *Journal of Experimental Psychology: General*, 122, 73-91.
- Murray, R. F., & Morgenstern, Y. (2010). Cue combination on the circle and the sphere. *Journal of Vision*, 10(11):15, 1-11. doi: 10.1167/10.11.15
- Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of cue integration in human navigation. *Current Biology*, 18, 689-693.
- Philbeck, J. W., & O'Leary, S. (2005). Remembered landmarks enhance the precision of path integration. *Psicologica*, 26, 7-24.
- Ratliff, K. R., & Newcombe, N. S. (2008). Reorienting when cues conflict: Evidence for an adaptive-combination view. *Psychological Science*, 19, 1301-1307.
- Shams, L., & Beierholm, U. R. (2010). Causal inference in perception. *Trends in Cognitive Sciences*, 14, 425-432.
- Shams, L., Kamitani, Y., & Shimojo, S. (2000). What you see is what you hear. *Nature*, 408, 788.
- Shettleworth, S. J., & Sutton, J. E. (2005). Multiple systems for spatial learning: dead reckoning and beacon homing in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, 31, 125-141.

- Taube, J. S., Muller, R. U., & Ranck, J. B. (1990). Head-direction cells recorded from the postsubiculum in freely moving rats. II. Effects of environmental manipulations. *Journal of Neuroscience*, *10*, 436-447.
- Tcheang, L., Bühlhoff, H. H., & Burgess, N. (2011). Visual influence on path integration in darkness indicates a multimodal representation of large-scale space. *Proceedings of the National Academy of Sciences of USA*, *108*, 1152-1157.
- Trullier, O., Wiener, S. I., Berthoz, A., & Meyer, J.-A. (1997). Biologically based artificial navigation systems: Review and prospects. *Progress in Neurobiology*, *51*, 483-544.
- Wehner, R., Michel, B., & Antonsen, P. (1996). Visual navigation in insects: Coupling of egocentric and geocentric information. *Journal of Experimental Biology*, *199*, 129-140.
- Welch, R. B., & Warren, D. H. (1980). Immediate perceptual response to intersensory discrepancy. *Psychological Bulletin*, *88*, 638-667.
- Yoder, R. M., Clark, B. J., & Taube, J. S. (2011). Origins of landmark encoding in the brain. *Trends in Neurosciences*, *34*, 561-571
- Yuille, A. L., & Bühlhoff, H. H. (1996). Bayesian decision theory and psychophysics. In D. Knill & W. Richards (Eds.), *Bayesian approaches to perception*. New York: Cambridge University Press.

FIGURE CAPTIONS

Figure 1 Homing task and hypothesized homing responses.

(a) Homing task. Participants walked from Start to Vertex 1 (Home), Vertex 2, and Vertex 3 (the response point), and then returned to the remembered Home location. When landmarks (stars) were shifted, homing could be based on PI alone (dashed black line), landmarks alone (dashed gray line), or their combination. Background reference grid = 1 m². (b) View of virtual environment from Start location, showing the Home pole with two proximal (left) or distal (right) landmarks. (c) Hypothetical response probabilities based on PI, LM, and their optimal integration. Arrows represent mean homing direction and spread of distribution reflects variability.

Figure 2 Responses of a sample participant in each group.

(a-c) Rows represent a participant from the Proximal LM, the Distal LM, and the Distal PI groups. Columns (left to right) represent the single-cue conditions, the combined condition, and the six landmark-shift conditions. Green circle = actual home location, coincident with response location predicted by PI; red diamond = response location predicted by landmarks.

Figure 3 Homing direction is dominated by a single cue rather than cue integration.

(a-c) Homing directions in each landmark shift condition for the three groups, where 0° is the true home direction. Dashed lines represent predicted homing direction based on PI, landmarks, and their optimal integration. Histograms indicate the distribution of homing

directions in each condition, with von Mises fits (VM fit) to the corresponding circular distributions; red circles represent the mean of the fitted distribution. **(d)** Observed and predicted circular mean homing direction for individual participants. Lines show robust linear fit of the data.

Figure 4 Mean homing variability is consistent with optimal integration prediction.

(a) Mean within-subject circular SD in the PI-alone, landmarks-alone (LM), and combined (Com) conditions, together with the predicted SD for the combined condition (Pred). **(b)** Mean circular SD in the landmark shift conditions, together with optimal integration predictions (shaded band = $M \pm 95\%$ CI). One participant in Distal PI group was excluded from this analysis due to unusually high variability (mean SD: 53° , range: $28-75^\circ$). * $P \leq .05$, ** $P < .01$, n.s. = not significant; error bars represent SE.

Figure 5 Homing variability for individual participants is consistent with optimal integration prediction.

Optimal integration predicts individual circular SDs in each landmark shift condition up to 90° , but not with large landmark shifts of 115° and 135° . ** $P < .001$. Black lines are best-fit linear regression lines.

How You Get There From Here:

Interaction of Visual Landmarks and Path Integration in Human Navigation

Mintao Zhao & William H. Warren

Brown University

ONLINE SUPPORTING INFORMATION

Supplementary Methods

1. Circular data analysis

Circular data analysis was performed using a Matlab toolbox for circular statistics (Berens, 2009). We used Equations 1 and 2 to predict homing direction and response variability respectively when PI and LM are optimally integrated (Murray & Morgenstern, 2010).

$$\theta_{PI+LM} = \theta_{LM} + \Delta - \arctan(\sin(\Delta), \kappa_{LM} / \kappa_{PI} + \cos(\Delta)) \quad (1)$$

$$\kappa_{PI+LM} = \sqrt{\kappa_{PI}^2 + \kappa_{LM}^2 + 2\kappa_{PI}\kappa_{LM} \cos(\Delta)} \quad (2)$$

where $\arctan(y, x)$ is the four-quadrant inverse tangent; θ and κ are mean homing direction and the parameter of concentration estimated from circular normal distribution fitting; Δ is angular landmark shift; and $\theta_{LM} + \Delta$ is predicted homing direction if participants completely follow landmarks (i.e., landmark prediction, see **Figure 3d**). So homing direction should be biased towards LM prediction when $\kappa_{LM} > \kappa_{PI}$, biased towards PI prediction $\kappa_{LM} < \kappa_{PI}$, and homing in between when $\kappa_{LM} = \kappa_{PI}$.

The observed and predicted response variability (i.e., κ) was transformed to circular standard deviation (σ) with Equation 3 (based on Eq. 2.3.2 and 16.4.3 in Batschelet, 1981), where $I(x)$ represents the Bessel function of first kind.

$$\sigma = \sqrt{2(1 - I_1(\kappa) / I_0(\kappa))} \quad (3)$$

2. Cluster analysis of bimodal responses

For each participant, homing directions at 115 and 135° shifts were clustered based on their normalized angular distances to the LM and PI predictions (i.e., z scores). Homing directions were treated as unimodal if one of the two cluster components had fewer than 2 data points, and bimodal otherwise. Homing directions in each component were fitted with circular normal distribution to estimate mean homing direction and response variability.

3. Linear data analysis

Linear data analysis revealed the same pattern of results as the circular data analysis (**Figure S4**). We used Equations 4 and 5 to predict mean homing direction (θ) and response variability (σ^2) (Ernst & Banks, 2002).

$$\theta_{PI+LM} = w_{PI}\theta_{PI} + w_{LM}\theta_{LM} \quad (4)$$

$$\sigma_{PI+LM}^2 = \sigma_{PI}^2\sigma_{LM}^2 / (\sigma_{PI}^2 + \sigma_{LM}^2) \quad (5)$$

Where w_{LM} and w_{PI} represent weights allocated to LM and PI cue respectively.

Assuming $w_{LM} = 1 - w_{PI}$, we could compute actual and predicted weights for landmarks (i.e., landmark reliance) using Equation 4, and compute actual and predicted response variability using Equation 5.

References

- Batschelet, E. (1981). *Circular statistics in biology*. New York: Academic Press.
- Berens, P. (2009). CircStat: A Matlab toolbox for circular statistics. *Journal of Statistical Software*, 31(10), 1-21.
- Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, 415, 429-433.
- Murray, R. F., & Morgenstern, Y. (2010). Cue combination on the circle and the sphere. *Journal of Vision*, 10(11):15, 1-11. doi: 10.1167/10.11.15

Supplementary Figures

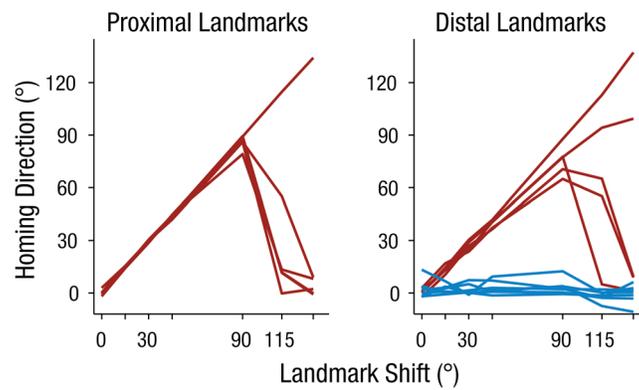


Figure S1 Homing directions as function of landmark shift for individual participants. Each line represents one participant. Note that participants tested with distal landmarks clearly show bimodal responses.

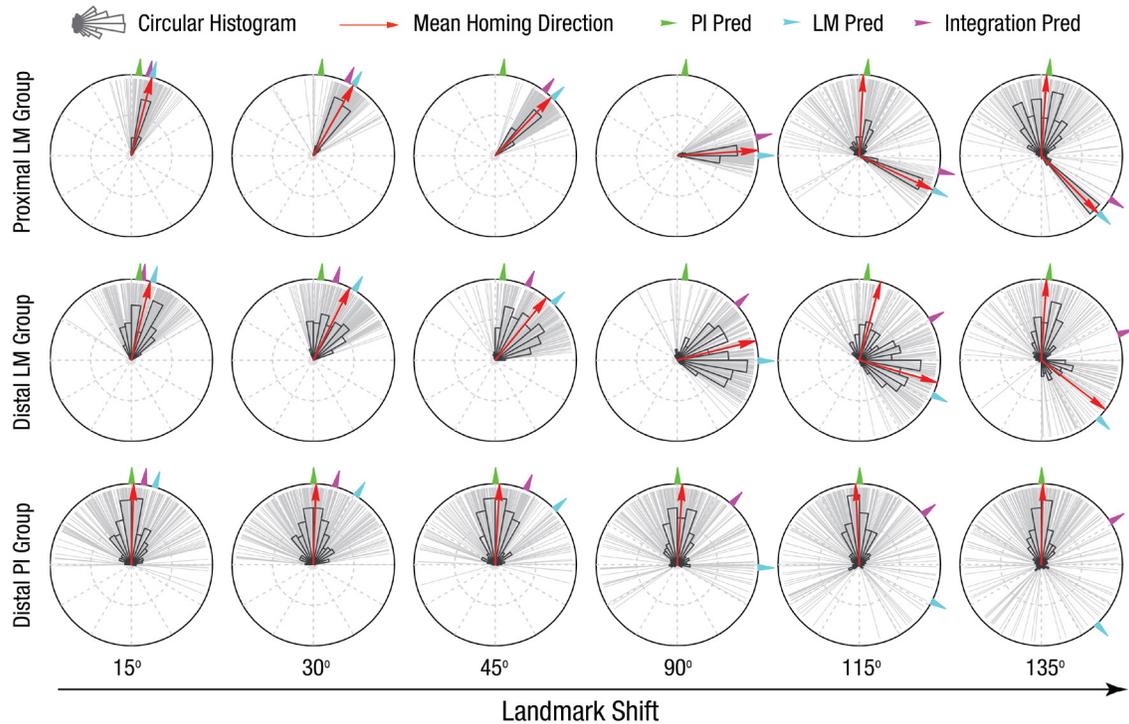


Figure S2. Raw data from individual trials and circular histogram of all homing directions in each landmark shift condition. Mean homing directions (red arrows) are consistent with either the LM prediction (blue triangle) or PI prediction (green triangle), but not the optimal integration prediction (purple triangle). Both Proximal LM and Distal LM groups relied on landmarks up to a 90° shift; then switched to rely on path integration. Distal PI group relied on path integration in all landmark shift conditions. North (up) direction represents target direction, gray lines indicate individual responses. None of the data set was distributed uniformly around the circle (all $Z > 38.74$, all $P < 1.85 \times 10^{-18}$, Rayleigh test).

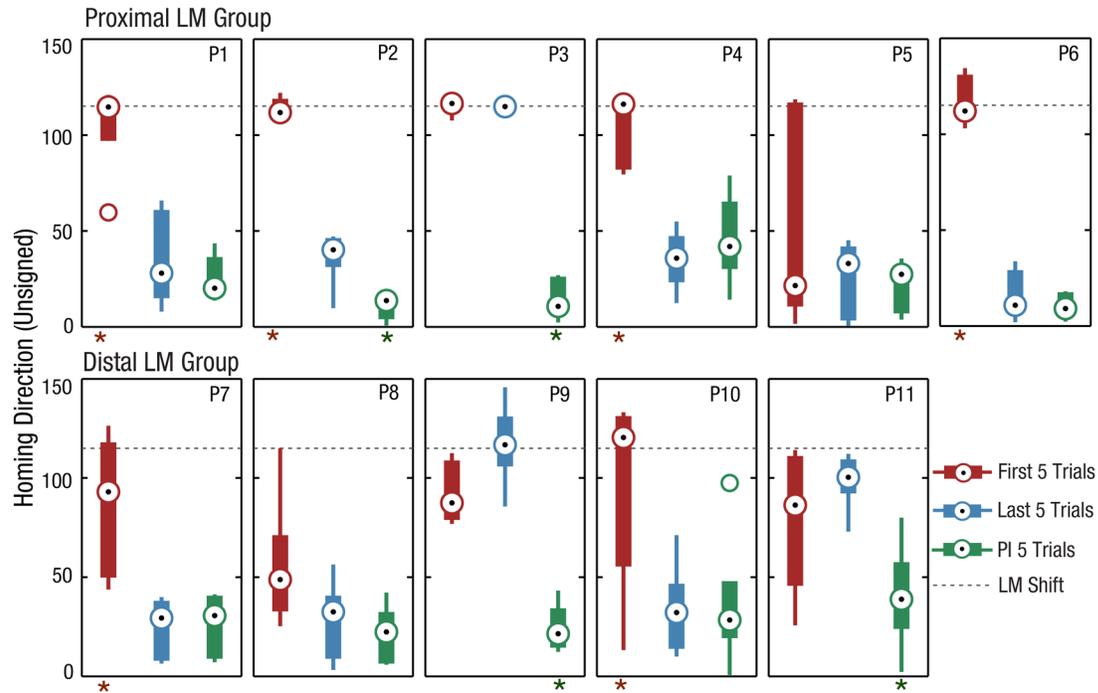


Figure S3. Switch from LM- to PI-dominance in 115° shift condition. Each panel represents data from one participant, including heading direction in the first 5 trials (red) and last 5 trials (blue) in the 115° shift condition, and the first 5 trials in the PI-only condition (green). Black dots indicate the median homing direction, colored boxes represent the 25th to 75th percentile, and whiskers the range of homing responses.

At the beginning of the 115° condition, all participants in Proximal LM and Distal LM groups followed the shifted landmarks in one or more trials (red), but only three of them (P3, P9, and P11) did so at the end (blue). Six participants (red asterisks) showed a significant difference in homing direction between the first five trials and the last five trials (all $F_{1,9} > 6.47$, all $P < 0.05$, Watson-Williams test). When comparing the last five trials in the 115° condition with the first 5 trials in the PI only condition (green), only four participants (green asterisks) showed a significant difference (all $F_{1,9} > 12.78$, all $P < 0.01$), whereas all others transitioned to PI-dominance.

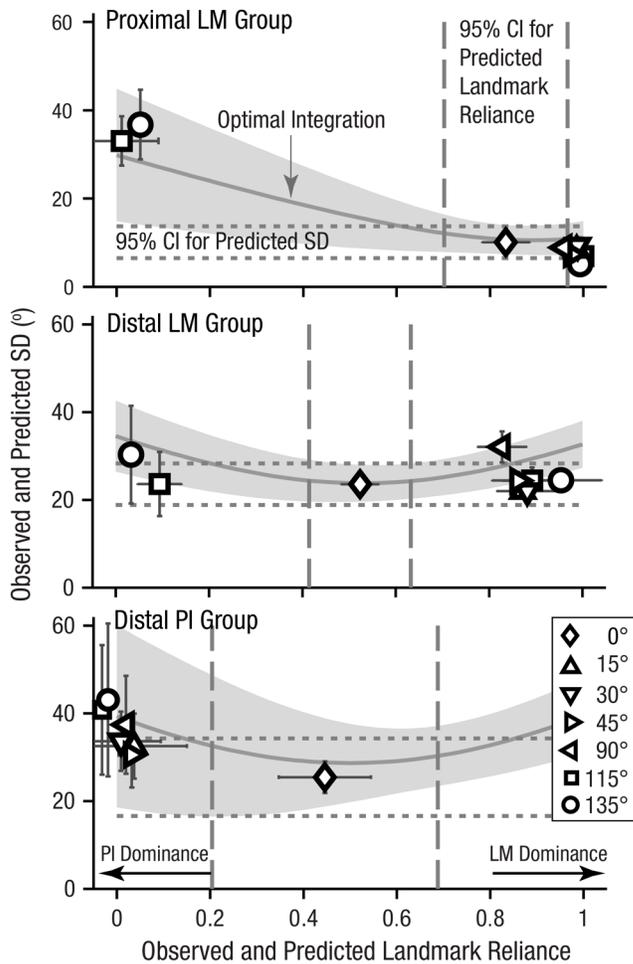


Figure S4. Linear data analysis shows cue dominance in homing direction and cue integration in response variability. X-axis represents hypothesized or actual landmark reliance (i.e., w_{LM} in Equation 4; 0 means ignoring landmarks and 1 means landmark dominance). Y-axis represents actual or predicted variability. Curved line and the shaded area are prediction of mean variability and its 95% confidence interval (CI). Variability data (shaped points) are generally consistent with optimal integration prediction (except 115° and 135° shifts), whereas homing direction data (as indexed by landmark reliance) are more consistent with cue dominance predictions. These results mirrored those reported in the main text using circular data analysis.