This paper is accepted for publication in Cognition

Environmental Stability Modulates the Role of Path Integration in Human Navigation

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Abstract

Path integration has long been thought of as an obligatory process that automatically updates

one's position and orientation during navigation. This has led to the hypotheses that path

integration serves as a *back-up system* in case landmark navigation fails, and a *reference system*

that detects discrepant landmarks. Three experiments tested these hypotheses in humans,

using a homing task with a catch-trial paradigm. Contrary to the back-up system hypothesis,

when stable landmarks unexpectedly disappeared on catch trials, participants were completely

disoriented, and only then began to rely on path integration in subsequent trials (Experiment 1).

Contrary to the reference system hypothesis, when stable landmarks unexpectedly shifted by

115° on catch trials, participants failed to detect the shift and were completely captured by the

landmarks (Experiment 2). Conversely, when chronically unstable landmarks unexpectedly

remained in place on catch trials, participants failed to notice and continued to navigate by path

integration (Experiment 3). In the latter two cases, they gradually sensed the instability (or

stability) of landmarks on later catch trials. These results demonstrate that path integration

does not automatically serve as a back-up system, and does not function as a reference system

on individual sorties, although it may contribute to monitoring environmental stability over

time. Rather than being automatic, the roles of path integration and landmark navigation are

thus dynamically modulated by the environmental context.

Keywords: navigation, path integration, landmark stability, back-up system, reference system

Environmental Stability Modulates the Role of Path Integration in Human Navigation

1 Introduction

Humans and a wide variety of nonhuman animals rely on two basic navigation mechanisms: landmark navigation and path integration (Barry & Burgess, 2014; Etienne & Jeffery, 2004; Gallistel, 1990; Trullier, Wiener, Berthoz, & Meyer, 1997). Landmark navigation refers to the process that uses visual features of the environment (e.g., landmarks, beacons, boundaries, or environmental geometry) for homing, reorientation, and wayfinding (Epstein & Vass, 2014; Foo, Warren, Duchon, & Tarr, 2005; Franz, Schölkopf, Mallot, & Bülthoff, 1998; Gillner, Weiss, & Mallot, 2008; Trullier et al., 1997). Path integration, on the other hand, refers to the process that keeps track of one's position and orientation by integrating the linear and angular components of self-motion, primarily based on idiothetic information (e.g., motor, proprioceptive, and vestibular information, Collett & Collett, 2000; Etienne & Jeffery, 2004; Kearns, Warren, Duchon, & Tarr, 2002; Loomis et al., 1993; Müller & Wehner, 1988). These two navigation systems thus largely depend on different sensory inputs (visual vs. idiothetic) and dissociable neural substrates (Epstein & Vass, 2014; Janzen & van Turennout, 2004; Wolbers, Wiener, Mallot, & Büchel, 2007; Yoder, Clark, & Taube, 2011).

Path integration has long been thought of as an obligatory process that functions continually whenever a navigator moves (Etienne & Jeffery, 2004; Etienne, Maurer, & Seguinot, 1996; Gallistel, 1990; Müller & Wehner, 1988). Such an automatic process might enable the path integration system to contribute to navigation in several ways. First, it has been proposed that

path integration serves as a *back-up system* for other navigation strategies (Cheng, Shettleworth, Huttenlocher, & Rieser, 2007; Collett & Collett, 2000; Shettleworth & Sutton, 2005). For instance, if landmark navigation were to fail for any reason, automatic path integration would enable the navigator to remain oriented to the environment. Second, it has been suggested that path integration serves as a *reference system* for other navigation cues (Buehlmann, Hansson, & Knaden, 2012; Cheng et al., 2007; Shettleworth & Sutton, 2005). Thus, a navigator could detect whether the locations of landmarks remain constant or change during a sortie (e.g., due to displacement or spatial aliasing). Third, path integration is known to guide navigation alone (e.g., homing in the dark) and can be combined with landmarks to improve navigation performance (Cheng et al., 2007; Collett, 2012; Nardini et al., 2008; Tcheang, Bülthoff, & Burgess, 2011; Zhao & Warren, 2015). Finally, path integration may continually relate the locations of landmarks to build up enduring spatial knowledge (Chrastil & Warren, 2013; Gallistel, 1990; McNaughton, Battaglia, Jensen, Moser, & Moser, 2006; Thrun, 2008). In sum, an automatic path integration process appears important to insure that the navigator remains oriented, detects unstable landmarks, and acquires spatial knowledge.

In the present study, we investigated the role of path integration during homing in humans, specifically, whether path integration serves as an *automatic* back-up and reference system during landmark navigation. Contrary to these two hypotheses, we find that the role of path integration as a back-up system is not automatic but is modulated by environmental stability. In addition, path integration does not appear to serve as a reference system that

accepts or rejects landmarks on an individual sortie, but it may contribute to a more general process that evaluates the stability of the environmental context.

1.1 Path integration as an automatic process

Evidence for automatic path integration comes primarily from research on animal navigation (Etienne et al., 1996; Müller & Wehner, 1988). Behaviorally, rodents and desert ants show a striking ability to return straight home after foraging on a complex outbound path, suggesting that the homing vector (i.e., relative direction and distance from one's current location to the home location) was continually updated en route (Müller & Wehner, 1988; Shettleworth & Sutton, 2005). At the neurophysiological level, self-motion continually changes the firing properties of the neural circuits underlying path integration, including neurons that are sensitive to place (O'Keefe & Nadel, 1978), head direction (Taube, Muller, & Ranck, 1990), and the relative direction and distance of places (i.e., grid cells, Hafting, Fyhn, Molden, Moser, & Moser, 2005). These results support the view that "path integration… seems to depend on a prewired system of information processing which functions automatically, whenever the subject locomotes" (Etienne et al., 1996, p206).

Similarly, humans update their current position relative to a starting point or goal location during blindfolded walking, implicating an analogous path integration system (Loomis et al., 1993; Kearns et al., 2002). Furthermore, it appears that human navigators cannot ignore their own movements during navigation (Klatzky, Loomis, Beall, Chance, & Golledge, 1998; May, 2004; May & Klatzky, 2000), suggesting that the integration of self-motion information is obligatory. For instance, using a triangle completion task, May and Klatzky (2000) asked

blindfolded participants to walk on a two-leg outbound path and then to return directly to their

starting location. In the critical *irrelevant walking* conditions, a 2-m backward or rightward

displacement was added to the outbound path, but participants were asked to ignore this

irrelevant walking during the homing response. However, they were unable to do so;

participants showed errors that were consistent with the prediction that all walked paths were

integrated. This result suggests that path integration is obligatory during physical locomotion.

Conversely, humans have difficulty incorporating imagined self-motion into path integration,

providing complementary evidence that path integration is anchored to self-motion information

(Klatzky et al., 1998; May, 2004; Rieser, 1989). Taken together, these results suggest that path

integration is automatically linked to physical locomotion.

Such evidence is consistent with the view that path integration is continually active

during human locomotion. However, these results only demonstrate that path integration is

closely tied to physical self-motion once the system is activated, in tasks such as blind walking

that require it for successful performance. They do not show that path integration is obligatory

when other navigation strategies are operative.

1.2 Interaction between path integration and landmark navigation

What is the contribution of path integration during landmark navigation? One

possibility is that path integration automatically updates the navigators' position and

orientation even when they are navigating by visual landmarks. In an insightful article, Cheng

et al (2007) proposed that "path integration continues to operate obligatorily in the

background" (p631) to serve two functions. First, path integration acts as a back-up system in

case landmark navigation fails, due to displaced or discrepant landmarks (see also Collett & Collett, 2000; Etienne et al., 1996). Second, it also serves as a reference system that detects such discrepancies, by keeping track of landmark locations during a sortie and "set[ting] limits on what are acceptable landmarks" (Cheng, et al, 2007, p634). If a landmark location is within the tolerance range of path integration it is accepted as stable, but if it is displaced too far from its original position, it is rejected as unstable and ignored.

Shettleworth and Sutton (2005) reported evidence for the back-up system and reference system hypotheses in animal navigation. They trained rats in a homing task with a salient beacon cue, and then tested their homing performance when the beacon either remained at the home location, was removed, or was shifted to a new location. When the beacon was removed, homing accuracy was similar to that when the beacon was visible at the home location. The authors concluded that path integration is continually active as a back-up system and takes over when landmarks become unavailable. When the beacon was shifted by 45° it captured the homing direction, but when the beacon was shifted by 90° the rats rejected it and returned home by path integration. We similarly found that humans rejected landmarks that were shifted by 115° from their original locations and navigated by path integration (Zhao & Warren, 2015). These findings appear to be consistent with the hypothesis that path integration also serves as a reference system to check whether landmarks are stable or unstable – although it is quite insensitive to landmark displacements. Note, however, that the rejection of landmarks in these experiments occurred after landmarks had been removed or displaced on multiple trials, creating an unstable environmental context. Riecke, van Veen, & Bülthoff (2002) similarly

reported homing by integration of optic flow when landmarks were replaced on multiple trials, although they did not provide idiothetic information. It is thus unknown if path integration served as reference system on the first such trial.

On the other hand, this 'landmark capture' effect has also been interpreted as evidence that landmarks reset the path integration system. Because path integration drifts and error accumulates rapidly (e.g., Loomis et al., 1993), a navigator can take an environmental 'fix' on visual landmarks and re-initialize the path integrator, thereby facilitating reorientation and self-localization (Etienne & Jeffery, 2004; Etienne, Maurer, Boulens, Levy, & Rowe, 2004; Valerio & Taube, 2012; see also Knierim & Hamilton, 2011). Covertly shifting a visual beacon not only captures an animal's homing behavior, but also induces a corresponding shift in the spatial tuning of underlying neural mechanisms (e.g., place cells, head direction cells, and grid cells; Hafting et al., 2005; Knierim, Kudrimoti, & McNaughton, 1998; Taube et al., 1990). Human navigation similarly exhibits landmark capture, such that visual landmarks completely dominate the homing direction with landmark shifts as large as 90°, whereas 115° shifts are rejected (Zhao & Warren, 2015; see also Foo et al, 2005). Landmark capture may result from navigators' prior experience in a largely stable environment, which leads a navigator to expect that landmarks remain stable during navigation. In addition, rapidly accumulating error in the path integration system may also privilege landmark-based navigation (Cheng et al., 2007; Collett & Collett, 2000; Loomis et al., 1993).

We point out that the demands of a reference system actually conflict with those of a resetting mechanism: a precise reference system should be sensitive to small landmark

discrepancies, whereas a resetting mechanism should tolerate large discrepancies and reorient

to the visual surround. Zhao & Warren (2015) recently estimated the discrimination threshold

of the human path integration system in the triangle completion task as about 47° ($\sqrt{2}\sigma_{PI}$, where

σ_{PI} represents the standard deviation of homing responses based on path integration alone,

Ernst & Banks, 2002; the threshold for navigation based on proximal landmarks is about 16°).

The finding that landmarks shifted by twice as much (90°) still capture homing behavior implies

that the resetting mechanism dominates and that path integration is, at best, a highly imprecise

reference system. Nonetheless, this observation does not rule out the possibility that path

integration is automatically running in the background during landmark navigation as a

backup system or a weak reference system (Cheng et al., 2007; Collett & Collett, 2000).

We propose that the role of path integration is not automatic but depends on the

environmental context. When navigating in environments with potentially unstable landmarks,

path integration might continually function as a back-up system. However, in environments

with stable landmarks that uniquely specify locations, a back-up system is unnecessary and

may be suppressed. Consistent with the independence of landmark navigation and path

integration, previous studies have shown that route following in humans (based on landmarks)

recruits different neural substrates from path integration (Hartley, Maguire, Spiers, & Burgess,

2003; Wolbers et al., 2007). Further, we suggest that path integration is too insensitive to serve

as a reference system that accepts or rejects landmarks on individual sorties. Unstable

landmarks could be detected by other means, such as a change in their visual configuration,

change in the relation among multiple environmental cues (Jacobs, 2002), or from basic spatial

relations (e.g., a landmark on one's left cannot remain on one's left after one turns around).

Finally, this raises the question of how a navigator assesses the stability of the environmental

context in which they are operating. To investigate these questions, one needs to test navigation

performance in stable and unstable environments, using a navigation task that does not require

path integration.

1.3 The present study

In the present study, we tested whether path integration plays an obligatory role during

human navigation by manipulating the stability of visual landmarks. Specifically, we

addressed three questions. First, does path integration automatically serve as a back-up system

in an environment with stable landmarks? Second, does path integration serve as a reference

system to detect unstable landmarks? And finally, do the roles of path integration and

landmark navigation change in an environment with chronically *unstable* landmarks?

To investigate these questions, we used a triangle completion task in an ambulatory

virtual environment, which allows covert manipulations of the visual environment that is

typically impossible in the real environment. We asked participants to walk on an outbound

path, and then to walk directly back to the designated 'home' location. Participants could base

this homing response on either path integration alone, visual landmarks alone, or both. To

probe the state of path integration, we used a catch trial paradigm, in which the landmarks

were manipulated on *catch trials* that occurred amidst a series of *standard trials* (Foo et al., 2005;

Shettleworth & Sutton, 2005). To provide a baseline for a normally functioning path integration

system, we also tested a final set of *baseline trials* with no visual landmarks, so participants were forced to rely on path integration alone to perform the task.

In Experiment 1 we tested the automatic back-up system hypothesis. During standard trials the landmarks remained in place throughout the trial, whereas during catch trials they were visible on the outbound path but disappeared unexpectedly prior to the homing response. Thus, participants had to fall back on path integration to return home successfully. By comparing catch trials with baseline trials, this design enabled us to test whether path integration is continually operating as a back-up system in the presence of stable landmarks. In Experiment 2 we tested the automatic reference system hypothesis. On catch trials, we covertly shifted the landmarks by 115°. Such a large landmark shift allowed us to test whether path integration is automatically detecting unstable landmarks. Conversely, in Experiment 3 the landmarks were chronically unstable, but unexpectedly remained in place on catch trials. This allowed us to test whether path integration is continually detecting acceptable stable landmarks, and whether the role of landmark navigation is modulated by the environmental context. Our results show that human path integration does not function as an automatic back-up system for landmark navigation, and may not function as a reference system at all; rather, the roles of path integration and landmark navigation are dynamically modulated by the environmental context.

2 Experiment 1: Is Path Integration an Automatic Back-up System?

Experiment 1 tested whether path integration functions as an automatic back-up system when navigating in environments with stable landmarks. Participants performed the homing task while the presence of visual landmarks was manipulated. On standard trials, three distinctive towers were visible and remained in fixed locations throughout the experiment. On four random catch trials, these towers were present on the outbound path but disappeared unexpectedly before the homing response. On the final baseline trials, no landmarks were present, requiring that participants use path integration from the beginning of each trial to perform the task. If path integration automatically updates the navigator's position and orientation, participants would simply fall back on path integration when the landmarks disappear on catch trials. Thus, the automatic back-up system hypothesis predicts comparable performance on catch trials and baseline trials. In contrast, if the presence of stable landmarks during standard trials downweights or completely suppresses the role of path integration as a back-up system, homing performance should be significantly worse on catch trials than on baseline trials.

2.1 Methods

2.1.1 Participants

Twelve people (5 men, 7 women; age 18-27) participated in the experiment. In this and subsequent experiments, the procedure was approved by local Institutional Review Board, and written consent was obtained from each participant before experiment.

2.1.2 Displays

Experiments were conducted in the Virtual Environment Navigation Lab at Brown University. The virtual environment was generated using Vizard software (WorldViz, CA), and presented in a head-mounted display (SR80-A HMD, Rockwell Collins, IA; field of view 63° × 53°, resolution 1280 x 1024 pixels per eye, refresh rate 60 Hz). Head position was tracked and recorded with a hybrid inertial/ultrasonic tracking system (InterSense, MA; sampling rate 60 Hz). The outbound walking path was marked by poles (10 cm radius, 1.5 m tall) that were presented one at a time (**Figure 1**). Three unique towers (a radio tower, a water tower, and an Eiffel-like tower, each about 2 m tall) served as proximal landmarks (Figure 1b). These towers were placed 5.5 m from the end of the path (vertex 3, **Figure 1a**), separated by 45°; their locations remained constant throughout the experiment, although the start and home locations varied across trials. The ground was textured with a grayscale Voronoi pattern and the sky was black.
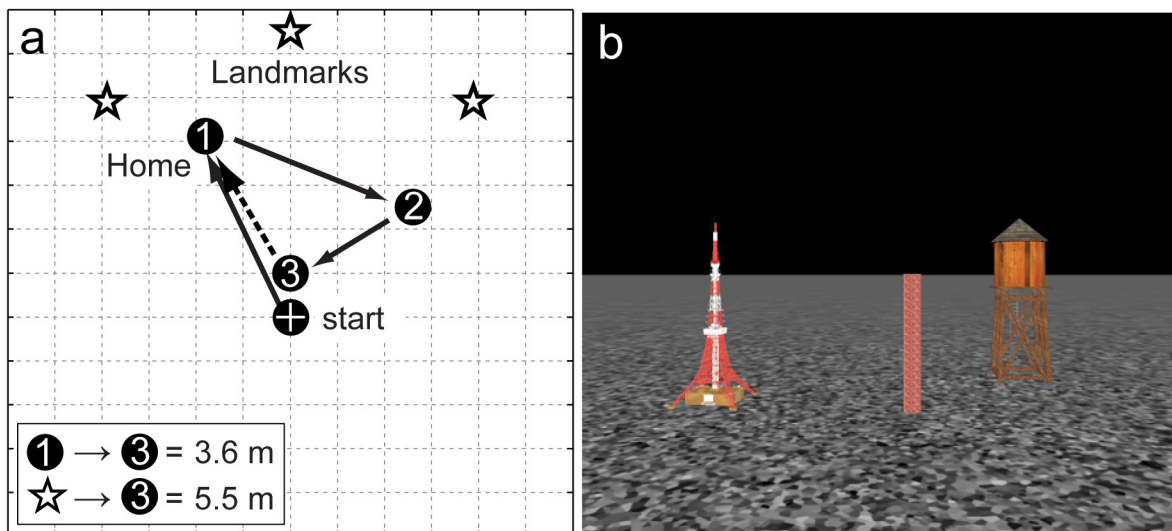

Figure 1

Twenty outbound paths with different configurations were created, five paths for each of four home locations. Different start locations were used for the five paths with the same home location. The end of the path was always located at the center of the tracking space. The required turn angle for a correct homing response (∠231 in **Figure 1a**) varied between 60 to 120° in steps of 15°, while the correct homing distance was always 3.6 m. The lengths of individual segments for the outbound path varied between 2 to 6.6 m.

2.1.3 Procedure

In each trial, colored poles were used to mark the starting point and the three vertices of the outbound path, which were presented one at a time. Participants stood at the starting point, facing the *home* location (indexed by a red pole, **Figure 1b**), and were instructed to remember its location and walk to the Home pole. The Home pole disappeared when the participant reached it, the next pole on the path appeared (at vertex 2), and turning instructions ("turn left" or "turn right") were presented via headphones. Participants turned their body until they faced the newly appeared pole, and then walked to the pole. This sequence repeated for vertex 3, so only one pole was visible at a time and the full outbound path was never visible simultaneously. When participants reached the end of the path (vertex 3), a homogeneous textured circular wall appeared for 8 s (10 m in diameter, 6 m in height, centered at response location), as in Zhao and Warren (2015). When the wall disappeared, participants were instructed to turn and walk directly to the remembered home location. They clicked a hand-held mouse to indicate that they reached the home location. The homing direction was measured as the vector from the vertex 3 to the location at which they clicked the mouse.

Each participant completed 56 homing trials, including four catch trials amid 44 standard trials, followed by eight baseline trials. The first eight standard trials were used as familiarization trials and were excluded from data analysis. These trials allowed participants to get comfortable in the virtual environment and to acquaint themselves with the homing task. On standard trials, the three landmarks remained in fixed positions relative to the start, home, and response locations throughout the trial (i.e., stable landmarks). On catch trials, the landmarks were present during the outbound path, but were covertly removed before the homing response. The removal of landmarks was triggered by participants' walking direction from vertex 2 to vertex 3. This insured that the landmarks were outside the HMD's field of view when they were removed, so participants could not *see* them disappear. Catch trials were randomly inserted into the standard trials, with the constraints that they occurred after at least eight standard trials (i.e., familiarization trials) and were separated by at least five standard trials. On baseline trials, no landmarks were presented. Half of the eight baseline trials used the same paths as on the catch trials, presented in the same order (hereafter called *matched baseline* trials), and the other four used randomly selected paths. Baseline trials were run in a block at the end of the session to avoid alerting participants to the possibility that the landmarks might not appear.

2.1.4 Data analysis

In this and subsequent experiments, *homing error* in each trial was calculated as the absolute difference between actual response direction and the correct home direction. Note that the chance performance corresponds to a homing error of 90°: if a participant is completely

disoriented, the absolute homing errors would be randomly distributed between 0° and 180°,

resulting in a mean homing error of 90°. To compare overall performance in each condition

(standard, catch, and baseline), we calculated the mean homing error for each condition across

participants. To examine performance on individual catch trials, we compared each catch trial

(1st to 4th) with its matched baseline trial. We report all significant statistics (α =.05), along with

effect size measured as either partial eta squared (η_p^2) for ANOVAs or Cohen's d for t-tests.

Bonferroni-corrected p values are reported for post hoc multiple comparisons. Mean homing

errors are reported with standard errors (i.e., $M \pm SE$).

2.2 Results

Homing errors for a trial sequence from one sample participant are presented in **Figure**

2a, which represents the general pattern of performance. It is apparent that error spiked on the

first catch trial (red triangles). Mean homing error was smallest in the standard condition,

larger in the baseline condition, and greatest on catch trials (**Figure 2b**). A one-factor repeated

measures ANOVA revealed a main effect of condition on homing error ($F(2, 22) = 33.55$, $p < .001$,

$\eta_p^2 = .75$). More importantly, mean homing error in the catch trials (44.19 $\pm$ 6.33°), when

landmarks unexpectedly disappeared before homing, was significantly greater than that in the

baseline trials (24.77 $\pm$ 5.03°), when participants knew beforehand that they could only rely on

path integration ($t(11) = 4.59$, $p = .002$, Cohen's $d = 1.33$). This result reveals that the path

integration system does not continually operate as a back-up system in an environment with

stable landmarks. Both catch trials and baseline trials had significantly greater errors than

standard trials (11.13 ± 3.89°; both $t \geq 6.05$, both $p < .001$, Cohen's $d \geq 1.75$), indicating that visual
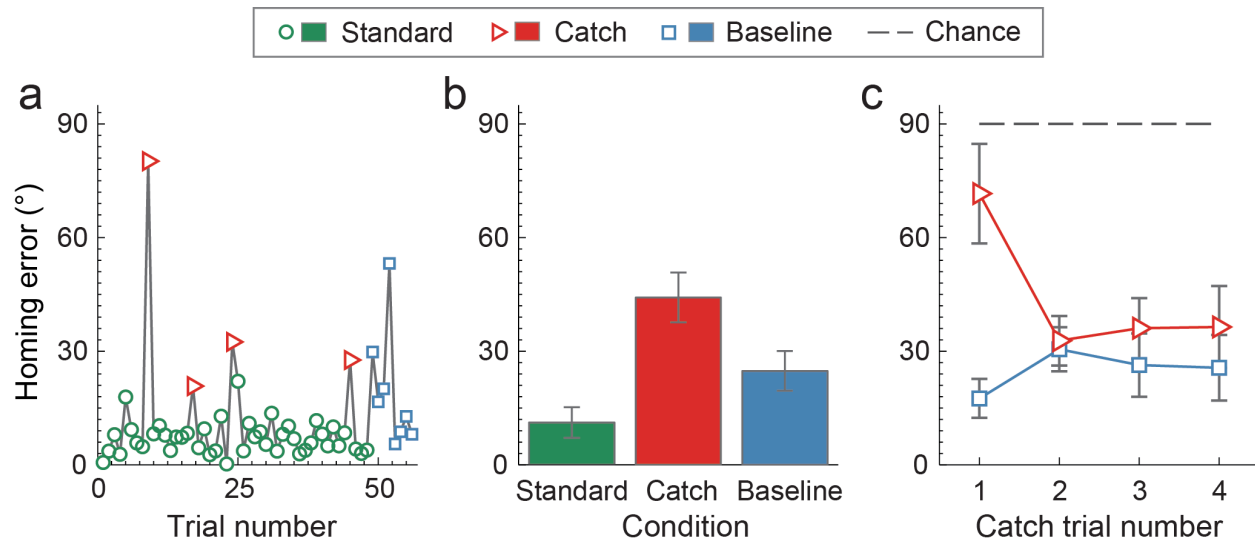
landmarks were exploited when available.

Figure 2

To examine individual catch trials more closely, mean homing error is plotted as a

function of catch trial number (1st to 4th) in **Figure 2c**. We compared the four catch trials with

their matched baseline trials in a two-way (2 conditions × 4 trials) repeated measures ANOVA,

yielding a main effect of condition ($F(1, 11) = 17.60$, $p = .001$, $\eta_P^2 = .62$), and a significant

interaction between trial number and condition ($F(3, 33) = 7.37$, $p < .001$, $\eta_P^2 = .40$). A separate

one-way ANOVA in each condition found a significant effect of trial number for catch trials

($F(3, 33) = 4.96$, $p = .006$, $\eta_P^2 = .31$), but not matched baseline trials ($F(3, 33) = 1.57$, $p = .216$, η_P^2

$= .12$). Post hoc comparisons revealed that only the first catch trial had a higher error than the

corresponding baseline trial ($t(11) = 4.83$, $p = .002$, Cohen's $d = 1.39$), whereas the subsequent

three catch trials returned to baseline levels (all $t \leq 1.32$, $p \geq .853$, Cohen's $d \leq .38$).

Most important, participants were completely disoriented the first time the landmarks

disappeared. Planned comparisons revealed that the homing error on the first catch trial (71.60

± 12.60°) did not statistically differ from the chance level (i.e., 90°, $t(11) = 1.46$, $p = .172$, Cohen's d

= .42). In contrast, all subsequent catch trials showed better than chance performance (all $t >$

5.17, $p < .001$, Cohen's $d > 1.49$), indicating that path integration kicks in as a back-up system

after only one instance of landmark disappearance.

2.3 Discussion

The results of Experiment 1 indicate that an environment in which landmarks remain

stable for repeated trials effectively suppresses the function of path integration as a backup

system. Yet a single instance of disappearing landmarks is sufficient to reactivate this system,

so path integration guides homing when landmarks disappear on subsequent trials. This

finding indicates that the role of path integration is modulated by the environmental context: it

is suppressed in an environment with stable landmarks, and reactivated after exposure to

unstable landmarks – in this case, landmarks that disappear and risk disorientation.

It might be objected that participants were simply confused the first time the landmarks

disappeared and performed poorly because they were distracted searching for the missing

landmarks. However, this is exactly the situation in which an automatic back-up system is

supposed to function, to maintain one's orientation when other navigation strategies fail. The

complete disorientation exhibited on the first catch-trial provides the best evidence that path

integration does not play this role, although it is quickly reactivated after one instance of

disorientation.

Experiment 1 thus shows that path integration does not serve as an automatic back-up navigation system. Nonetheless, it remains possible that path integration serves as an automatic reference system, enabling the navigator to detect unstable landmarks. Despite its relative imprecision, path integration may be useful as a reference system because it is unaffected by conditions that can undermine landmark navigation, such as large displacements or confusable visual landmarks (Cheng et al., 2007; Mallot & Gillner, 2000). We addressed this issue in Experiment 2.

3 Experiment 2: Is Path Integration an Automatic Reference System?

Experiment 2 examined whether path integration automatically operates as a reference system to detect landmark instability during individual sorties. This hypothesis is suggested by previous experiments that put visual landmarks in conflict with path integration. When landmarks are shifted by 90° or more, nonhuman animals begin to ignore them and rely on path integration (Knierim et al., 1998; Shettleworth & Sutton, 2005). Similarly, humans switch from landmark navigation to homing by path integration alone when visual landmarks are shifted by 115° or more (Zhao & Warren, 2015). These results imply that sufficiently discrepant landmarks are detected by a (rather imprecise) reference system and rejected as unstable. However, the rejection may also be attributable to an unstable environmental context, because the navigators had been exposed to multiple trials in which landmarks were shifted or disappeared.

To test whether path integration serves as an automatic reference system, we unexpectedly shifted visual landmarks on catch trials, using the same paradigm as in Experiment 1. Specifically, landmarks were covertly shifted 115° to the left or right prior to the homing response in catch trials (**Figure 3**). We previously found that the 115° shift is well above the estimated discrimination threshold of path integration in this task (i.e., 47°), and elicits a switch from landmark navigation to path integration when presented in blocked trials (Zhao & Warren, 2015). In the present experiment, the landmarks remained in place on standard trials, and were shifted on four randomly-interspersed catch trials. To estimate homing accuracy when a shift is detected, on baseline trials we shifted landmarks 115° left or right and told participants in advance that the landmarks would change position on every trial. This instruction was intended to act like an explicit "reference system" that alerted participants to landmark instability, prompting them to reject the landmarks and rely on path integration. If path integration functions similarly as a reference system, we would expect comparable performance on catch trials and baseline trials. In contrast, if path integration does not automatically serve as a reference system, participants would fail to detect the landmark shifts and continue to rely on landmark navigation, leading to larger errors on catch trials than baseline trials.

3.1 Methods

3.1.1 Participants

Twelve people (5 men, 7 women, age 18-32) participated in the experiment. None of them participated in Experiment 1.

3.1.2 Displays, procedure, and data analysis

The method was identical to that of Experiment 1 with the following exceptions. First, on catch trials, all three landmarks were covertly shifted en bloc 115° to the left or the right about vertex 3 as the participant walked from vertex 2 to 3 (**Figure 3**). Second, in the baseline condition, landmarks were also shifted en bloc ±115°, but before beginning the baseline trials participants were explicitly told, "All towers that appear in the first view will always change their locations before the homing response; they will not stay at their original locations throughout a trial."

As in Experiment 1, homing error was computed as the absolute difference between actual response direction and the correct home direction. Due to technical problems, five trials failed to elicit the planned landmark shift, including two catch trials (participants 1 and 12) and three non-matched baseline trials (participants 1, 3, and 7). These trials were excluded from data analysis.
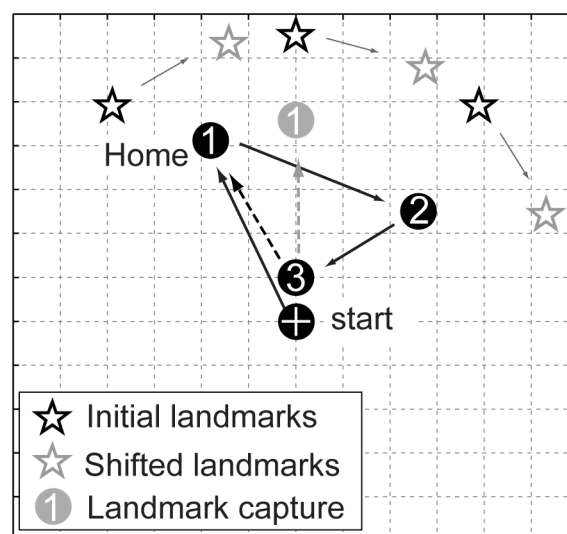
Figure 3

3.2 Results

Homing error on each trial for one sample participant is plotted in **Figure 4a**, which is

representative of the pattern of performance across participants. Participants generally

followed the shifted landmarks on catch trials. Mean homing error was greatest on catch trials,

smallest in the standard condition with stable landmarks, and in between in the baseline

condition (**Figure 4b**), as confirmed by a one-factor repeated measures ANOVA ($F(2, 22) = 57.76$,

$p < .001$, $\eta_p^2 = .84$). More crucially, the mean homing error on catch trials ($100.44 \pm 5.61°$) was

close to the shift angle of 115°, and significantly greater than the error on baseline trials when

participants knew the landmarks would shift ($46.04 \pm 10.78°$; $t(11) = 5.73$, $p < .001$, Cohen's $d =$

1.65). Thus, path integration did not automatically function as a reference system to detect the
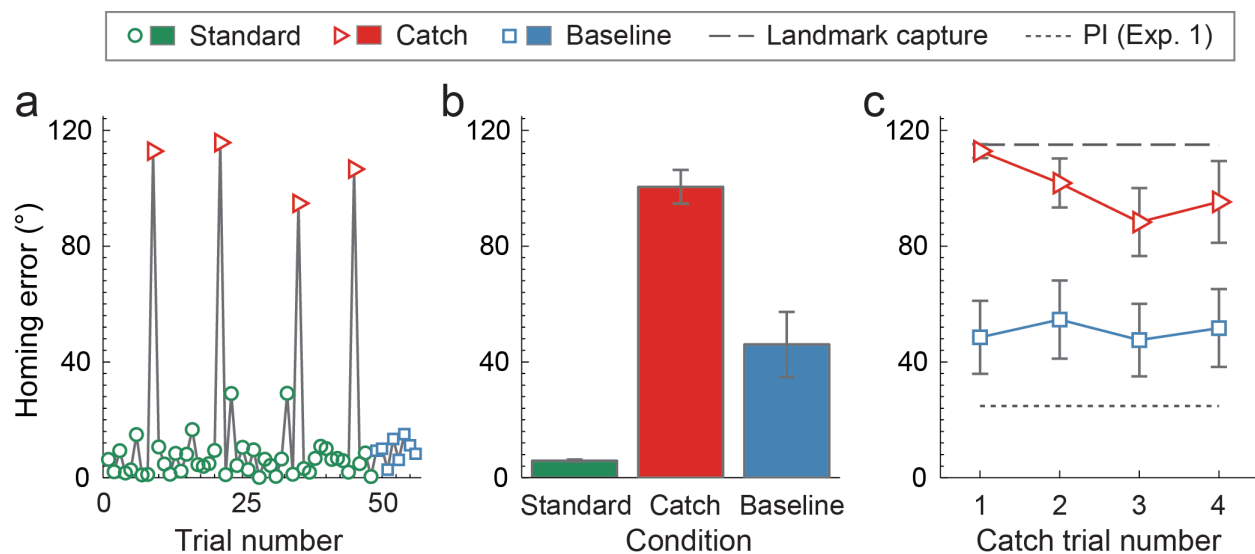
shifted landmarks.

Figure 4

Performance on individual catch trials confirmed that homing was dominated by the shifted landmarks (**Figure 4c**). A 2 (condition) by 4 (trial number) two-way repeated measures only revealed a significant main effect of condition ($F(1, 9) = 24.79$, $p < .001$, $\eta_{P}^2 = .73$), showing greater homing error on catch trials than on matched baseline trials. Post hoc comparisons revealed a significant difference between the first three catch trials and the matched baseline trials (all $t \geq 3.42$, $p \leq .026$, Cohen's $d \geq .99$), yet less so in the last catch trial ($t(10) = 2.76$, $p = .081$, Cohen's $d = .83$). Moreover, planned contrasts revealed that only the third catch trial exhibited significantly lower homing error than predicted by landmark capture (i.e., 115°, dashed line in **Figure 4c**; $t(10) = 2.39$, $p = .038$, Cohen's $d = .72$), whereas the other three were all captured by landmarks (all $t \leq 1.63$, $p \geq .13$, Cohen's $d < .47$). Conversely, when comparing to the mean homing error observed with path integration alone (i.e., 24.77°, dotted line in **Figure 4c**, based on baseline trials in Experiment 1), all catch trials showed greater homing error (all $t > 5.24$, $p < .001$, Cohen's $d > 1.58$). Thus, although landmark capture eroded in later catch trials, participants did not reject the landmarks and switch to navigation by path integration.

To determine what underlies the weakened landmark capture on later catch trials, we examined the behavior of individual participants over the four catch trials. If path integration serves as a reference system, shifted landmarks should be detected and rejected on each catch trial; or less strongly, if path integration contributes to monitoring environmental stability, they should at least heighten sensitivity to unstable landmarks on subsequent catch trials and precipitate a switch to path integration. Yet there is little evidence of this pattern. We adopted a criterion of landmark capture for individual homing responses of $M \pm 1.96\sigma_{LM}$ (**Figure 5**,

shaded area), where M is the homing direction predicted by landmark capture ($M = 115°$), and

σ_{LM} is the standard deviation of response directions when homing by landmarks alone ($\sigma_{LM} =$

11.09°, according to the 'proximal' landmarks condition in Zhao & Warren, 2015). This range

should therefore include 95% of individual homing errors captured by landmarks (i.e., 95%

confidence limits). As shown in **Figure 5**, seven of the 12 participants followed the landmarks

on all catch trials (left panel), three departed from landmarks for one or two trials but then

changed back (middle panel), while only two rejected landmarks and switched to path

integration (right panel). There is thus little evidence that individual participants regularly

detected and rejected shifted landmarks within single catch trials, or became increasingly
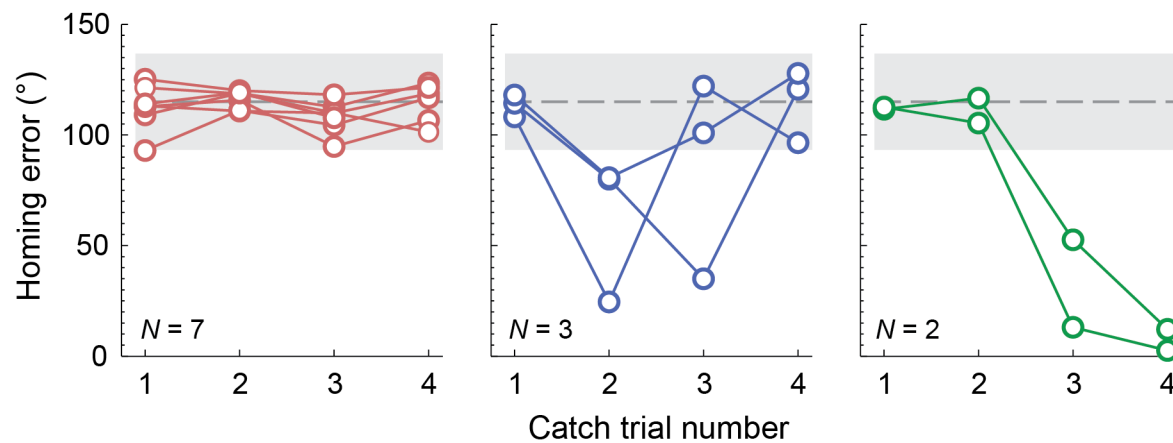
sensitive to unstable landmarks over catch trials.

Figure 5

Finally, we note that both catch trials and baseline trials exhibited greater homing error

than standard trials (5.90 ± 0.39°, both $t > 3.76$, $p \le .009$, Cohen's $d \ge 1.09$, **Figure 4b**), indicating

that participants tended to follow the shifted landmarks despite being explicitly told that they

were unstable. Conversely, all four matched baseline trials showed significantly lower homing

error than predicted by landmark capture (**Figure 4c**, all $t > 4.68$, $p < .001$, Cohen's $d > 1.35$), demonstrating that participants were only partially influenced by the landmarks when told they were unstable.

3.3 Discussion

Experiment 2 indicates that human path integration does not serve as an automatic reference system to detect unstable visual landmarks. On the first two catch trials, homing responses were completely captured by shifted landmarks, even though the 115° shift was well above the discrimination threshold of the human path integration system (47°). This finding demonstrates that path integration failed to detect and reject discrepant landmarks in individual trials, contrary to the reference system hypothesis.

Landmark capture appeared to erode in the third and fourth catch trials, suggesting that sensitivity to unstable landmarks may have gradually increased. However, discrepant landmarks were not rejected on these trials and participants did not generally switch to homing by path integration. Individual subject data revealed that most (10/12) participants relied on landmarks during all catch trials or changed back to them, while only two participants switched to path integration. This pattern of results indicates that exposure to unstable landmarks over four catch trials did not generally activate path integration as a reference system, or even heighten sensitivity to discrepant landmarks.

A reanalysis of Zhao and Warren's (2015) data confirms that, even when participants were continually exposed to ±115° landmark shifts in a block of 40 consecutive trials, only two of six participants abruptly switched from landmark navigation to path integration, while the

others either gradually converged to path integration over many trials or remained captured by the landmarks (Appendix **Figure A1**). There is thus little evidence that path integration systematically functions as a reference system to reject landmarks on individual sorties, or is activated by exposure to unstable landmarks, although it may contribute to a process that gradually senses environmental instability over multiple trials.
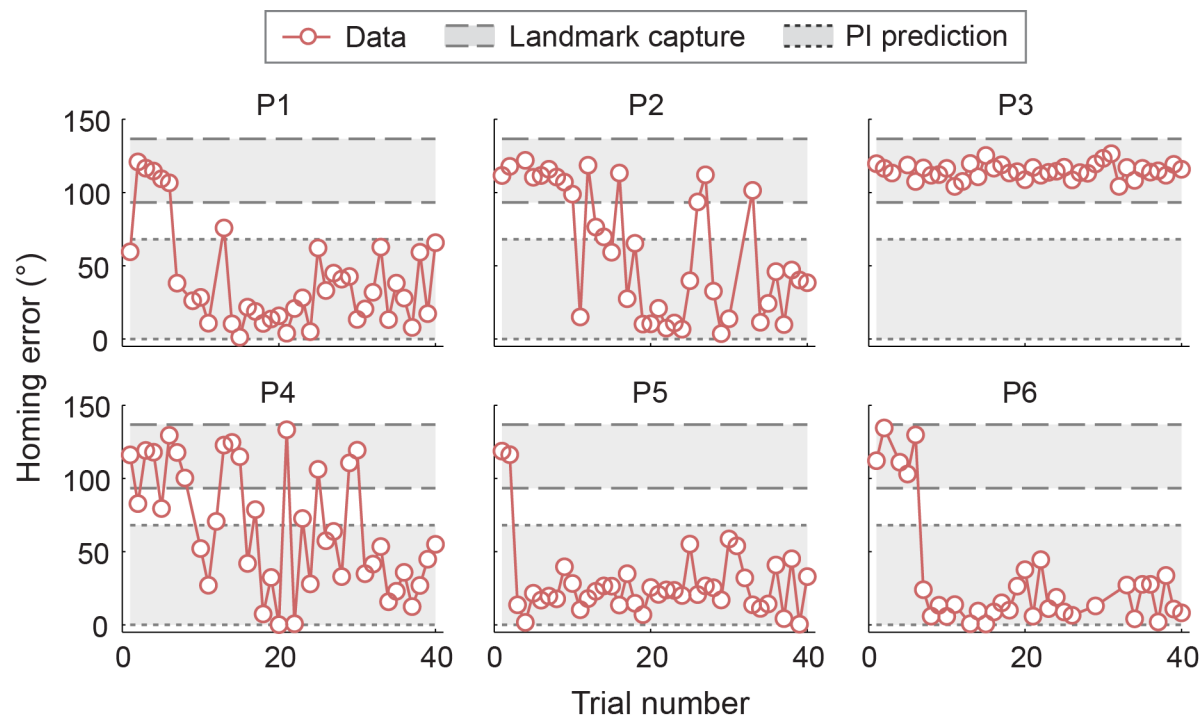

Figure A1

Experiments 1 and 2 demonstrate that, in an environment with *stable* landmarks, navigation is guided by the landmarks while path integration is suppressed as a back-up system, and does not serve as a reference system. Conversely, in Experiment 3 we ask whether an environment with chronically *unstable* landmarks modulates the roles played by path integration and landmark navigation.

4 Experiment 3: Path Integration and Landmark Navigation in an Unstable Environment

Experiment 3 examined whether, in an unstable environment, path integration automatically operates as a reference system to detect and accept stable landmarks, or whether landmark navigation is suppressed and all landmarks rejected. In contrast to Experiments 1 and 2, where landmarks were primarily stable, we presented chronically unstable landmarks on standard trials, but unexpectedly stable landmarks on catch trials. Specifically, on standard trials, the three landmarks in the initial view were semi-randomly repositioned before the homing response, changing their spacing but preserving their cyclic order. This manipulation presented visibly unstable landmarks within each trial, therefore promoting homing by path integration. In contrast, on the four catch trials, the landmarks remained fixed in their initial positions, so they were visibly stable throughout the trial. Finally, on baseline trials no landmarks were present, requiring homing by path integration. Such a design allowed us to test whether a path integration system that actively guides navigation also serves as a reference system to identify stable landmarks, or whether all landmarks are rejected and landmark navigation is generally suppressed in an unstable environment.

If path integration serves as a reference system, then homing errors should be lower on catch trials than on baseline trials because stable landmarks would be detected and used to guide navigation, whereas the latter are guided by path integration alone. In contrast, if an unstable environment suppresses landmark navigation, then landmarks would be routinely

rejected. In this case, stable landmarks on catch trials would go unnoticed and navigation would be guided by path integration, yielding homing error comparable to baseline trials.

4.1 Methods

4.1.1 Participants

Twelve people (7 men, 5 women, age 18-26) participated in the experiment. None of them participated in Experiment 1 or 2.

4.1.2 Displays, procedure, and data analysis

The methods were identical to those of Experiment 1, with the following exceptions. First, on standard trials, the locations of the three landmarks visible from the start point were changed prior to the homing response. The three initial landmark locations were determined by non-repeated random sampling from 11 predefined locations (i.e., -50° to 50° in steps of 10° around the center of the gray arc, **Figure 6**), and their shifted locations were sampled from 19 predefined locations (i.e., -90° to 90° in steps of 10° along the whole gray arc, **Figure 6**). The initial and shifted landmark locations were not identical, and the changed configuration of landmarks was readily detectable visually. Second, on catch trials, the landmarks remained fixed in their original locations throughout the trial. As in Experiment 1, no landmarks were presented on baseline trials. Again, homing error was computed as the absolute difference between actual response direction and the correct home direction.
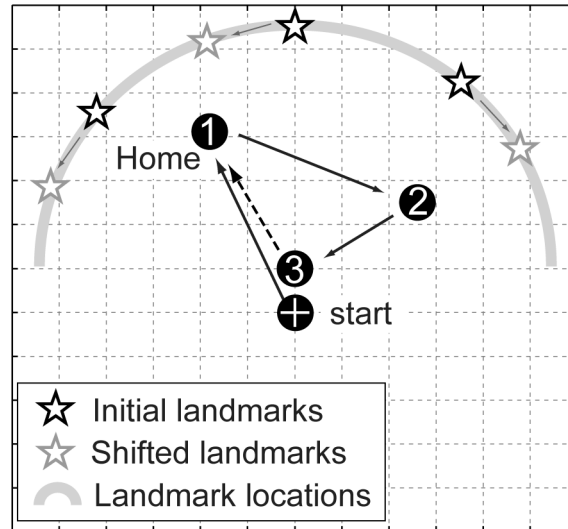
Figure 6

4.2 Results

Homing errors for a trial sequence from one sample participant appear in **Figure 7a**, which illustrates the general pattern. In the context of chronically unstable landmarks, participants generally ignored the stable landmarks on catch trials. Mean homing errors were similar in all three conditions (**Figure 7b**, $F(2, 22) = 2.06$, $p = .151$, $\eta_P^2 = .16$). More importantly, mean homing error on catch trials with stable landmarks ($21.30 \pm 2.94°$) was indistinguishable from that on baseline trials without landmarks ($18.94 \pm 3.29°$, $t(11) = .88$, $p = 1$, Cohen's $d = .25$). This result implies that participants, on average, failed to detect the stable landmarks on catch trials and continued to navigate by path integration. There was also no statistical difference between standard trials ($24.03 \pm 2.99°$) and baseline trials, or between standard trials and catch trials (both $t(11) \leq 2.29$, $p \geq .127$, Cohen's $d \leq .66$), implying that participants primarily relied on path integration in all three conditions.
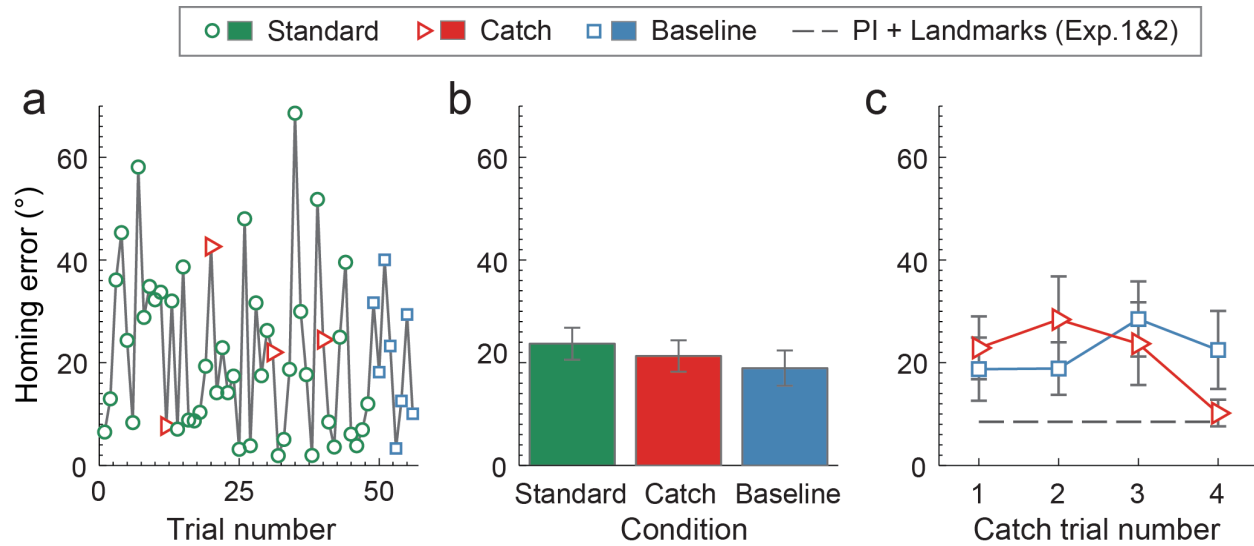
Figure 7

Mean homing errors on the individual catch trials and matched baseline trials are illustrated in **Figure 7c**. A two-way (2 conditions × 4 trials) repeated measures ANOVA found no main effects or an interaction (all $F < 1.53$, $p > .226$, $\eta_P^2 \leq .12$), again suggesting that participants relied on path integration in catch trials. Post hoc comparisons showed no statistical differences between any of the four catch trials and the corresponding baseline trials (all $t(11) < 1.77$, $p \geq .421$, Cohen's $d < .51$), suggesting that chronically unstable landmarks led the navigation system to routinely reject landmarks, even when they were actually stable on catch trials.

However, there was a marginally significant decreasing linear trend in homing error across the four catch trials ($F(1, 11) = 3.61$, $p = .084$, $\eta_P^2 = .25$). Participants appeared to gradually sense the stable landmark configuration such that by the last catch trial homing error was reduced to the level previously observed with stable landmarks. To assess this, we compared

performance on the catch trials to the mean performance on the standard trials with stable

landmarks from Experiments 1 and 2 (8.51 ± 1.99°, dashed line in **Figure 7c**). The first three

catch trials showed significantly greater homing errors (all $t \geqslant 2.51$, $p < .017$, Cohen's $d \geqslant .83$),

but the fourth catch trial did not (10.20 ± 2.48°, $t(34) = .51$, $p = .615$, Cohen's $d = .17$). This result

suggests that navigators gradually sensed the stable landmarks and used them to navigate on

the fourth catch trial.

4.3 Discussion

The results of Experiment 3 provide further evidence that path integration does not

function as a reference system. Despite the use of path integration for homing, it did not

simultaneously serve as a reference system to identify stable landmarks; rather, landmarks were

rejected overall. Participants did not take advantage of stable landmarks in early catch trials.

By the fourth catch trial, though, sensitivity to stable landmarks had increased and participants

used them to guide homing. This heightened sensitivity may be attributed to the fact that the

invariant configuration of landmarks during catch trials was visually specified.

More broadly, Experiment 3 offers complementary evidence that the role of landmark

navigation is modulated by the environmental context. Just as a stable environment

temporarily suppressed the functions of path integration in Experiments 1 and 2, leading to

reliance on landmark navigation, here a chronically unstable environment temporarily

suppresses landmark navigation and leads to reliance on path integration. Previous research

has also reported that humans and animals change from landmark navigation to path

integration due to cue conflicts produced by large landmark shifts (Barry, Hayman, Burgess, &

Jeffery, 2007; Etienne, Lambert, Reverdin, & Teroni, 1993; Shettleworth & Sutton, 2005; Whishaw & Tomie, 1997; Zhao & Warren, 2015; see also Ratliff & Newcombe, 2008). But in the present experiment there was no cue conflict during catch trials, for visual landmarks and path integration were congruent – yet landmarks were ignored in early catch trials nonetheless. This persistence reflects the suppression of landmark navigation by landmark instability on the preceeding trials. Conversely, the emergence of landmark navigation in later catch trials implies an increased sensitivity to stable landmarks due to gradually sensing stable configurations on previous catch trials. These observations confirm that environmental stability is monitored over multiple trials, and are inconsistent with the hypothesis that path integration serves as a reference system that accepts or rejects landmarks on individual sorties.

5 General Discussion

The present study investigated whether path integration is an obligatory process that functions as an automatic back-up and reference system during human navigation. Our results indicate, first, that the role of path integration as a back-up system is not automatic but is dynamically modulated by the environmental context. In Experiment 1 we found that, in an environment with stable landmarks, path integration is suppressed as a back-up system – but it is rapidly reactivated if landmarks are revealed as potentially unstable (i.e. disappear). This result provides clear evidence that the back-up system function of path integration is modulated by environmental stability.

Second, path integration does not appear to serve as a reference system that accepts or rejects particular landmarks. We find that path integration is ineffective at detecting stable and unstable landmarks during an individual sortie. Experiment 2 showed that in a stable environment, path integration failed to reject highly discrepant landmarks (±115° shifts) on individual trials. Conversely, Experiment 3 showed that in a chronically unstable environment, path integration failed to accept constant landmark configurations on individual trials. These results are inconsistent with the hypothesis that path integration serves as a reference system that detects discrepant or stable landmarks.

Moreover, exposure to shifted landmarks over four catch trials in Experiment 2 did little to increase sensitivity to discrepancies on subsequent trials, implying that a reference system based on path integration was not activated by instability. In contrast, stable landmarks *were* gradually sensed over four catch trials in Experiment 3, due to their visual configuration rather than a cue conflict with path integration. These observations raise the question of how environmental (in)stability is sensed over multiple sorties. We consider these conclusions in more detail.

5.1 Landmark stability modulates path integration as a back-up system

Contrary to the back-up system hypothesis (Cheng et al., 2007; Collett & Collett, 2000; Shettleworth & Sutton, 2005), in an environment with stable landmarks, path integration does not automatically serve as a back-up navigation system. When normally stable landmarks unexpectedly disappeared for the first time (catch trials in Experiment 1), participants became completely disoriented. They exhibited significantly greater homing errors than with path

integration alone (baseline trials), and were no different from the chance level. This

disorientation reveals that path integration does not automatically update the navigator's

position and orientation; rather, a stable environment acts to suppress its role as a back-up

system.

However, path integration is quickly activated as a back-up system if landmark

navigation fails. Participants only became disoriented on the first catch trial. On subsequent

catch trials, homing accuracy recovered to the baseline level, indicating that path integration

started operating as a back-up system. These results provide evidence that human path

integration is not obligatory, but modulated by environmental stability: it is suppressed as a

back-up system by stable landmarks, reactivated when potential instability is revealed, and

takes over as the primary navigation system when landmarks are chronically unstable

(Experiment 3).

5.2 Path integration does not function as a reference system

Contrary to the reference system hypothesis (Cheng et al., 2007; Shettleworth & Sutton,

2005), path integration does not serve to identify discrepant and acceptable landmarks. In a

stable environment (Experiment 2), participants failed to detect a 115° landmark shift on the

first two catch trials and were completely captured by the landmarks, even though the

discrepancy was more than twice the discrimination threshold of path integration (47°, Zhao &

Warren, 2015). Conversely, in a chronically unstable environment (Experiment 3), participants

rejected landmarks that were actually stable on the first two catch trials, and completely relied

on path integration for homing.   These results indicate that path integration does not function

as an automatic reference system that checks landmark stability on individual sorties.

Further, exposure to unstable landmarks on catch trials (Experiment 2) did not activate

such a reference system, for discrepant landmarks were not generally rejected on subsequent

catch trials. Only 17% of participants switched to path integration by the fourth catch trial. We

thus found little evidence to support the hypothesis that path integration serves as a reference

system, either automatic or modulated. Indeed, we believe this follows from the contrary

demands on a reference system that detects discrepant landmarks and a mechanism that uses

landmarks to reset the path integrator (Zhao & Warren, 2015). Path integration tolerates large

landmark shifts of 90° or more because the navigator relies on a stable environment to

compensate for accumulated error in path integration. Consequently, a reference system based

on path integration would, perforce, be highly insensitive to landmark shifts.

5.3 Sensing environmental stability

The view that the function of navigation systems depends on the environmental context

presumes a means of monitoring that context. How, then, does a navigator determine what

kind of environment they are in? In particular, what information specifies the general

(in)stability of the environment over multiple sorties?

It is known that repeated landmark shifts that exceed the resetting range of the path

integrator yield a change from homing by landmarks to homing by path integration (Cheng et

al., 2007; Etienne et al., 1996; Shettleworth & Sutton, 2005). Our previous results indicate that a

sufficiently large discrepancy (115°) on multiple trials eventually leads to the rejection of

landmarks, although this seldom occurs in a single trial (Zhao & Warren, 2015, Appendix

Figure A1). Another means of sensing environmental (in)stability is the visual configuration of

landmarks. In Experiment 3, chronically unstable landmarks were repositioned during a

standard trial, thereby changing their visual configuration, whereas stable landmarks on catch

trials maintained an invariant configuration throughout the trial. This configuration constancy

within a sortie was gradually sensed over the four catch trials, yielding a switch to landmark

navigation on the last catch trial.

Navigators may have developed other strategies for sensing environmental (in)stability

as well, such as detecting change in landmark position relative to the visual surround, change in

the relation among several multimodal cues (Cheng et al., 2007; Jacobs, 2002), or change in the

environment *between* sorties due to spatial learning. We pursue this question in a subsequent

study. In sum, monitoring the environmental context does not depend on a path-integration-

based reference system that detects discrepancies within a single sortie, but on perceptual

strategies that sense environmental (in)stability over multiple sorties.

5.4 Comparison to animal navigation

The present results are consistent with a strong cross-species similarity in navigation

systems. Similar to observations of navigation in mammals (e.g., Etienne et al., 1993; Etienne et

al., 2004; Knierim et al., 1998; Shettleworth & Sutton, 2005; Whishaw & Tomie, 1997), apparently

stable landmarks reset the orientation of the human path integrator, whereas detectably

unstable landmarks precipitate a switch from landmark navigation to path integration.

Moreover, analogues to the neural networks that support animal navigation (i.e., place cells,

grid cells) have been identified in human brain (Ekstrom et al., 2003; Jacobs et al., 2013). These results imply a common solution for the interaction of path integration and landmarks in human and animal navigation (Zhao & Warren, 2015). Specifically, visual landmarks reset the path integrator by reorienting the head direction cell system, the grid cell system, and the directional coordinates of the place cell system (Knierim & Hamilton, 2011; Valerio & Taube, 2012; Yoder et al., 2011).

Despite this behavioral similarity, it is possible that navigation in animals is less influenced by the environmental context than we find in humans. It has been argued that animal path integration automatically provides a back-up system (e.g, Collett & Collett, 2000; Shettleworth & Sutton, 2005; Wehner, 2003) and a reference system that detects whether visual and odor landmarks are stable (Buehlmann et al., 2012; Cheng et al., 2007; Müller & Wehner, 2010; Shettleworth & Sutton, 2005). However, it is unclear whether the back-up and reference system hypotheses would survive critical tests in animals, such as those in the present study. Recently, Knight et al (2014) showed that large landmark shifts (140°) capture the heading direction signal in naïve rats, but not in experienced rats that were previously exposed to landmark shifts – contrary to an automatic reference system. Such results suggest that the function of path integration in nonhuman animals may be modulated by environmental context as well.

5.5 Comparison to artificial navigation system

Many artificial or robotic navigation systems are inspired by findings about biological navigation system (Hübner & Mallot, 2007; Kuipers, 2000; Milford & Wyeth, 2010; Trullier, et

al., 1997). Like human and animal navigators, these systems face the same problems of acquiring spatial knowledge about the environment and localizing/orienting themselves, and attempt to solve them by combining path integration or "odometry", vision-based navigation, and other strategies. Because most artificial navigation systems assume the environment is stable (but see Milford & Wyeth, 2010), they do not consider back-up system and reference system functions for path integration. However, they often use visual input to recalibrate the path integrator, which accumulates errors due to odometry noise. This is equivalent to the process of visual landmarks resetting the path integration system in biological navigation.   In these artificial systems the phenomenon of landmark capture may also be due to other processes besides resetting. For instance, landmark capture could result from erroneous visual self-localization/orientation (Hübner & Mallot, 2007; Milford & Wyeth, 2010), or from causal associations between visual input and action generation (i.e., control laws; Kuipers, 2000; see also Mallot & Gillner, 2000).

5.6 Conclusions

We find that the role of path integration in human navigation is not automatic but is dynamically modulated by the environmental context. First, path integration does not automatically serve as a back-up system, for it is suppressed in a stable environment and is reactivated when landmarks disappear. Second, path integration does not serve as a reference system that accepts or rejects particular landmarks, although it may contribute to sensing environmental instability over time. Third, a stable environment suppresses path integration as the primary navigation system and leads to landmark navigation, whereas an unstable

environment suppresses landmark navigation and gradually leads to reliance on path

integration. Precisely how the navigator monitors the stability of the environmental context

remains to be determined.

Acknowledgements

Appendix

To further examine the role of path integration as a reference system, we reanalyzed our

previous data from the condition that proximal landmarks were continually shifted ±115° for 40

homing trials (Zhao & Warren, 2015). As shown in **Figure A1**, only two of six participants (P5

and P6) abruptly switched from landmark navigation to path integration; one (P3) continually

followed landmarks; and three (P1, P2 and P4) gradually shifted to path integration over

multiple trials. At the end, five of six participants were homing by path integration.
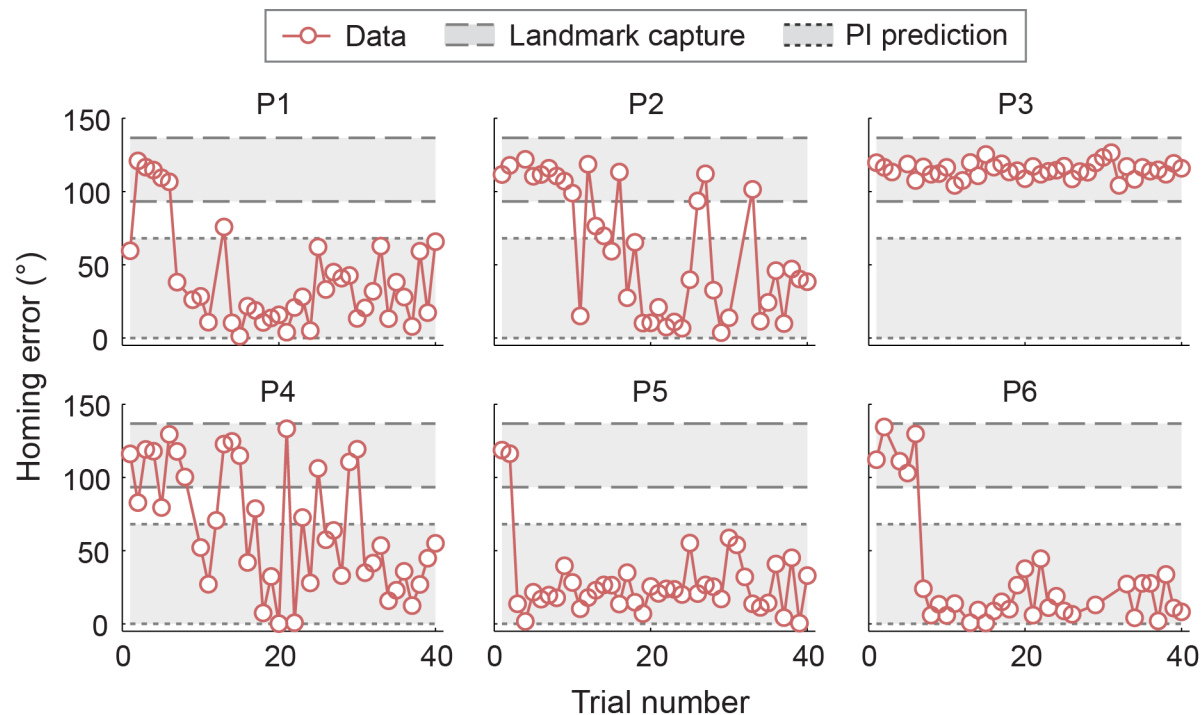
Figure A1. Homing error for individual participants when proximal landmarks are shifted 115°

for 40 trials. Area between dashed lines represents landmark capture (similar to Figure 5); area

between dotted lines shows path integration prediction (i.e., between 0 and $M + 1.96\sigma_{PI}$).

References

Barry, C., & Burgess, N. (2014). Neural mechanisms of self-location. *Current Biology, 24*, R330-R339.

Barry, C., Hayman, R., Burgess, N., & Jeffery, K. J. (2007). Experience dependent rescaling of entorhinal grids. *Natural Neuroscience, 10*, 682-684.

Buehlmann, C., Hansson, B. S., & Knaden, M. (2012). Path integration controls nest-plume following in desert ants. *Current Biology, 22*, 645-649. doi:10.1016/j.cub.2012.02.029

Cartwright, B. A., & Collett, T. S. (1982). How honey bees use landmarks to guide their return to a food source. *Nature, 295(5850),* 560-564.

Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. J. (2007). Bayesian integration of spatial information. *Psychological Bulletin, 133*, 625-637.

Chrastil, E.R. & Warren, W.H. (2013) Active and passive spatial learning in human navigation: Acquisition of survey knowledge. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 39*, 1520-1537.

Collett, M. (2012). How navigational guidance systems are combined in a desert ant. *Current Biology, 22*, 927-932.

Collett, T. S., & Collett, M. (2000). Path integration in insects. *Current Opinion in Neurobiology, 10*, 757-762.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. (2003). Cellular networks underlying human spatial navigation. *Nature, 425*, 184-187.

Epstein, R.A., & Vass L. K. (2014). Neural systems for landmark-based way-finding in humans. *Philosophical Transactions of the Royal Society B, 369:20120533*.

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature, 415*, 429-433.

Etienne, A. S., & Jeffery, K. J. (2004). Path integration in mammals. *Hippocampus, 14*, 180-192.

Etienne, A. S., Lambert, S. J., Reverdin, B., & Teroni, E. (1993). Learning to recalibrate the role of dead reckoning and visual cues in spatial navigation. *Animal Learning & Behavior, 21*, 266-280.

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.

Etienne, A. S., Maurer, R., & Seguinot, V. (1996). Path integration ln mammals and its interaction with visual landmarks. *Journal of Experimental Biology, 199*, 201-209.

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.

Franz, M. O., Schölkopf, B., Mallot, H. A., & Bülthoff, H. (1998). Where did I take that snapshot? Scene-based homing by image matching. *Biological Cybernetics, 79*, 191-202.

Gallistel, C. R. (1990). *The organization of learning*. Cambridge, MA: MIT Press.

Gillner, S., Weiss, A. M., & Mallot, H. A. (2008). Visual homing in the absence of feature-based landmark information. *Cognition, 109*, 105-122.

Hafting, T., Fyhn, M., Molden, S., Moser, M.-B., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature, 436*, 801-806.

Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: distinct neural bases of route following and wayfinding in humans. *Neuron, 37*, 877-888.

Hübner, W., & Mallot, H. A. (2007). Metric embedding of view-graphs: A vision and odometry-based approach to cognitive mapping. *Autonomous Robots, 23*, 183-196.

Jacobs, J., Weidemann, C. T., Miller, J. F., Solway, A., Burke, J. F., Wei, X. X., . . . Kahana, M. J. (2013). Direct recordings of grid-like neuronal activity in human spatial navigation. *Nature Neuroscience, 16*, 1188-1190.

Jacobs, R. A. (2002). What determines visual cue reliability? *Trends in Cognitive Sciences, 6*, 345-350.

Janzen, G., & van Turennout, M. (2004). Selective neural representation of objects relevant for navigation. *Nature Neuroscience, 7*, 673-677.

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.

Klatzky, R. L., Loomis, J. M., Beall, A. C., Chance, S. S., & Golledge, R. G. (1998). Spatial updating of self-position and orientation during real, imagined, and virtual locomotion. *Psychological Science, 9*, 293-298.

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.

Knight, R., Piette, C. E., Page, H., Walters, D., Marozzi, E., Nardini, M., … Jeffery, K. J. (2014) Weighted cue integration in the rodent head direction system. *Philosophical Transactions of Royal Society B, 369: 20120512*.

Kuipers, B. (2000). The Spatial Semantic Hierarchy. *Artificial Intelligence, 119*, 191-233.

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: Assessmetn of path integration ability. *Journal of Experimental Psychology: General, 122*, 73-91.

Mallot, H. A., & Gillner, S. (2000). Route navigation without place recognition: What is recognised in recognition-triggered responses? *Perception, 29, 43-55.*

May, M. (2004). Imaginal perspective switches in remembered environments: Transformation versus interference accounts. *Cognitive Psychology, 48*, 163-206.

May, M., & Klatzky, R. L. (2000). Path integration while ignoring irrelevant movement. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26*, 169-186.

McNaughton, B.L., Battaglia, F.P., Jensen, O., Moser, E.I., & Moser, M.-B. (2006). Path integration and the neural basis of the 'cognitive map'. *Nature Reviews Neuroscience, 7*, 663-678.

Milford, M., & Wyeth, G. (2010). Persistent navigation and mapping using a biologically inspired SLAM system. *International Journal of Robotics Research, 29*, 1131-1153.

Müller, M., & Wehner, R. (2010). Path Integration provides a scaffold for landmark learning in desert ants. *Current Biology, 20*(15), 1368-1371.

Müller, M., & Wehner, R. (1988). Path Integration in desear ants, *Cataglyphis fortis*. *Proceedings of the National Academy of Sciences of the USA, 85*, 5287-5290.

Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of cue integration in human navigation. *Current Biology, 18*, 689-693.

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Oxford University Press.

Ratliff, K. R., & Newcombe, N. S. (2008). Reorienting when cues conflict: Evidence for an adaptive-combination view. *Psychological Science, 19*, 1301-1307.

Riecke, B. E., van Veen, H. A. H. C., & Bülthoff, H. H. (2002). Visual homing is possible without landmarks: A path integration study in virtual reality. *Presence-Teleoperators and Virtual Environments, 11*, 443-473.

Rieser, J. J. (1989). Access to knowledge of spatial structure at novel points of observation. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 15*, 1157-1165.

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., Müller, 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., Bülthoff, 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.

Thrun, S. (2008). Simultaneous localization and mapping. In M. E. Jefferies & W-K. Yeap (Eds.), *Robotics and cognitive approaches to spatial mapping* (pp. 13-41). New York, NY: Springer.

Valerio, S. & Taube, J. S. (2012). Path integration: how the head direction signal maintains and corrects spatial orientation. *Nature Neuroscience, 15*, 1445–1453

Wehner, R. (2003). Desert ant navigation: how miniature brains solve complex tasks. *Journal of Comparative Physiology A, 189*, 579-588.

Whishaw, I. Q., & Tomie, J. A. (1997). Piloting and dead reckoning dissociated by fimbria-fornix lesions in a rat food carrying task. *Behavioural Brain Research, 89*, 87-97.

Wolbers, T., Wiener, J. M., Mallot, H. A., & Büchel, C. (2007). Differential recruitment of the hippocampus, medial prefrontal cortex, and the human motion complex during path integration in humans. *Journal of Neuroscience, 27*, 9408-9416.

Yoder, R. M., Clark, B. J., & Taube, J. S. (2011). Origins of landmark encoding in the brain. *Trends in Neurosciences, 34*, 561-571.

Zhao, M. & Warren, W. H. (2015). How you get there from here: Interaction of visual landmarks and path integration in human navigation. *Psychological Science, in press.* doi: 10.1177/0956797615574952.

Figure Captions

Figure 1. Homing task in an ambulatory virtual environment. (a) Exemplar homing task. Solid

arrow lines represent walking path from start to the end of path (vertex 3). Dashed arrow line

represents correct homing response. Grids in the background represent 1 m². (b) Screen shots

of virtual environment with two of the three visual landmarks; pole denotes the home location.

Figure 2. Homing error as a function of trial condition and trial number in Experiment 1. (a)

Homing errors of one sample participant. (b) Mean homing error on trials with stable

landmarks (standard trial), landmark disappear (catch trial), and no landmarks (baseline trial).

(c) Homing errors in individual catch trials and the matched baseline trials. Error bars are

standard errors (SE).

Figure 3. Schematic illustration of landmark shift in Experiment 2. Landmarks are shifted en

bloc to the left or right around vertex 3, producing a shifted home location (i.e., landmark

capture).

Figure 4. Homing error as a function of trial condition and trial number in Experiment 2. (a)

Homing errors of one sample participant. (b) Mean homing error on trials with stable

landmarks (standard trial), shifted landmarks (catch trial), and shifted landmarks that were

alerted in advance (baseline trial). (c) Homing error in individual catch trials and the matched

baseline trials. Dashed line represents landmark capture; dotted line represents homing error

based on path integration alone (i.e., baseline trials in Experiment 1). PI = path integration.

Figure 5. Homing error on the four catch trials for individual participants. Three patterns of

responses were observed based on whether participants (a) continually relied on landmarks on

all catch trials, (b) departed from landmarks on one or two trials and changed back, or (c)

switched to path integration over the course of four catch trials. Dashed line represents

landmark shift (i.e., 115°); shaded area represents predicted range of landmark catch, which

should include 95% of individual homing errors when homing by landmarks.

Figure 6. Schematic illustration of unstable landmarks used in Experiment 3. Individual

landmarks were moved from their initial locations to randomly selected new locations before

response. Possible landmark locations distributed along the gray arch in steps of 10°.

Figure 7. Homing error as a function of trial condition and trial number in Experiment 3. (a)

Homing errors of one sample participant. (b) Mean homing error on trials with unstable

landmarks (standard trial), stable landmarks (catch trial), and no landmarks (baseline trial). (c)

Homing errors in individual catch trials and the matched baseline trials. Dashed line represents

mean homing error based on both path integration and landmarks (i.e., baseline trials in

Experiments 1 and 2). PI = path integration.