Accepted in Journal of Experimental Psychology: Learning, Memory, and Cognition

Disrupted Orientation After Path Integration by Absence of Anticipated Prevalent Spatial Views

Yue Chen, Weimin Mou

Department of Psychology, University of Alberta

Author's Note

This work was partially supported by NSERC and Alberta Innovates fundings provided to Weimin Mou. We thank Advait Gulawani, Craig Neaves, Faroza Samiuddin, Jasmin Chan, Niel Jansen Van Rensburg, Shuier Wei and Yueyi Qiu for their contribution to data collection.

Database: https://doi.org/10.7939/r3-effv-6j83

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. This study was not preregistered. Data and experimental materials are available upon reasonable request.

Correspondence concerning this article should be addressed to Yue Chen or Weimin Mou, P217 Biological Sciences Bldg., Department of Psychology, University of Alberta, Edmonton, Alberta, Canada, T6G 2E9. Contact: chen27@ualberta.ca or wmou@ualberta.ca

Abstract

Two previous studies indicated that removing expected landmarks disrupts homing, a new phenomenon concerning interplay between path integration and landmark-based navigation. This study systematically investigated when this disruption occurs, which spatial representations are disrupted, and whether lessening landmark prevalence mitigates this disruption. In immersive virtual environments, against three landmarks, participants learned the location of a home object (Experiments 2&3), plus two additional objects (Experiment 1), or plus four additional objects (Experiments 4&5). They then navigated an outbound path originating from the home object. After participants' views were blocked, landmarks were revealed for nine standard paths/trials but removed in a subsequent catch trial, except in Experiment 3 where a curtain kept landmarks concealed. In Experiment 5, landmarks were rotated instead of being removed in the second catch trial. Participants replaced the home object in standard trials but all objects in catch trials. Baseline trials, which were identical to the catch trials except for no landmarks throughout the trials, followed catch trials. The results showed larger homing errors in first catch trials than baseline trials when landmarks were removed (Experiment 2) but not when the curtain concealed the landmarks (Experiment 3). For experiments with multiple objects, participants' represented position and heading were calculated based on the replaced and correct locations. Experiment 1 showed disrupted homing and heading estimates but intact position estimates, while Experiments 4&5 showed no disruption. Additionally, participants followed rotated landmarks in Experiment 5. These findings, provide a comprehensive picture of interplay between path integration and landmarks in familiar environments.

Key words: spatial views, self-localization, orientation, path integration, piloting

1. Introduction

During navigation, individuals use either their self-motion cues including optic flow or familiar landmarks to determine their locations and orientations relative to important items (e.g., home) in their environment. The navigation method based on self-motion cues is referred to as path integration and the method based on landmarks is referred to as piloting (Gallistel,1990; Gallistel & Matzel, 2013; Loomis et al., 1999; Philbeck et al., 2001; Mou & Wang, 2015). Over the past two decades, human navigation studies have showed that people can use each method separately, combine the estimates from each method in a Bayesian manner, or prefer estimates from piloting over those from path integration when there are significantly discrepancies between them (see Mou & Qi, 2024; Newman et al., 2023 for reviews). Most previous studies have intermixed trials with different available cues (i.e., path integration only, landmark only, and both cues). It led to experimental environments that did not accurately reflect everyday-life environments where familiar landmarks are constantly available. Thus, the interaction between piloting and path integration in navigation within familiar environments, where landmarks are constantly available, remains insufficiently examined and understood.

Inspired by the pioneer study of Zhao and Warren (2015a, Experiment 1), Chen and Mou (2024) proposed two hypotheses theorizing the interaction of path integration and piloting in familiar environments. The first hypothesis, known as the suppression hypothesis, stipulates that in familiar environments where stable landmarks are constantly available, people suppress path integration. This hypothesis aligns with findings that landmarks tend to dominate over path integration (Etienne & Jeffery, 2004; Foo et al., 2005; Mou & Zhang, 2014; Zhang & Mou, 2017; Zhao & Warren, 2015b). When stable landmarks are constantly available, estimates from path integration become apparently useless and then inefficient since path integration demands attention and working memory resources (Amorim et al., 1997; Wang et al., 2006).

The second hypothesis, the updating-spatial-views hypothesis, suggests that during navigation within a familiar environment, people use path integration to update the spatial views of important items (e.g. landmarks, home) in their environment to facilitate place/scene recognition (Simons & Wang, 1998; Zhang et al., 2011) and resolve ambiguity among visually similar items in different locations (Etienne et al., 1998; Sharp et al., 1990). This hypothesis draw inspiration from the discovery of the spatial view cells in the primate hippocampus (Rolls, 1999, 2023). Spatial view cells fired when a monkey looked at a specific area of the environment, regardless of its location and head orientation. Notably, these cells fired even when the actual view of the environment was blocked by a curtain, indicating that primates anticipate spatial views when observing their environment.

Zhao and Warren (2015a, Experiment 1) developed an elegant research paradigm to investigate how piloting and path integration jointly influence human navigation in familiar environments with constantly available landmarks. They used three types of trials: standard, catch, and baseline trials. In all trials, participants first observed the home location and walked to it (learning phase), then followed an outbound path with two segments originating from the home (outbound phase), and finally returned to the home (homing phase) after briefly having their view of the environment obstructed. Participants underwent multiple standard trials, where landmarks were visible throughout the trials, to establish an expectation of seeing landmarks during the homing phase. In a sequent catch trial, landmarks were presented in the learning and outbound phases but were unexpectedly removed in the homing phase. For comparison, the baseline trials, presented after the catch trials, featured no landmarks at any point during the trial.

Zhao and Warren's (2015a, Experiment 1) results showed that the absolute mean homing angular error in the first catch trial was significantly larger than that in the matched baseline trial (i.e., using the same walking path as in the first catch trial). This difference, however, disappeared for the following paired catch and baseline trials. Zhao and Warren (2015a) conjectured that in an environment with constantly available landmarks, path integration might have been suppressed. Thus, the sudden removal of landmarks will require participants to rely solely on spatial representations created by the previously suppressed path integration, resulting in the worse homing performance in the first catch trial than the matched baseline trial, in which no landmarks were presented to suppress path integration. After the first catch trial, participants expected that landmarks could be removed, which mitigated the suppression of path integration in subsequent catch trials. Hence, homing performance in the later catch trials became comparable to that in their matched baseline trials.

Chen and Mou (2024, Experiment 1b) first replicated Zhao and Warren's Experiment 1, employing a very similar design but with two changes. In the learning phase, participants learned a target object placed at the home. In the homing phase, instead of walking back to the home, participants were asked to replace the home object at its original location. Despite these changes, this experiment replicated the main findings of Zhao and Warren's experiment 1, showing a larger homing angular error in the first catch trial than the matched baseline trial.

Chen and Mou (2024) proceeded to differentiate the updating-spatial-views hypothesis from the suppression hypothesis in their following experiments (Experiments 2-4). They replaced a homing task with a recognition task in catch and matched baseline trials. Specifically, in the homing phase of catch trials, instead of asking participants to replace the home object after the removal of landmarks, they presented two groups of landmarks or home objects. In the correct group, the landmarks or the home object remained in their original locations. In the rotated group, the landmarks or the home object were rotated around the participants' testing position. Participants then recognized the correct landmarks/targets from the rotated ones. The results showed that recognition performance in the first catch trial was comparable to the matched baseline trials. Therefore, Chen and Mou (2024) concluded that path integration was not suppressed in the outbound phase of the first catch trial. Instead, participants updated the spatial views of the landmarks and targets during the outbound phase. These anticipated spatial views were used to remove the spatial ambiguity of the correct and rotated landmarks/targets. To account for the disrupted homing estimates in the first catch trial of their Experiment 1b and Zhao and Warren's Experiment 1, Chen and Mou attributed it to the stark mismatch between the real and anticipated views of the environment in the homing phase. While participants anticipated seeing landmarks, the empty ground disoriented participants and disrupted the updated spatial representations from path integration that could otherwise be used for homing.

Chen and Mou (2024) provided the initial evidence, showing that spatial representations updated by path integration in the catch trial can support recognition, thereby supporting the updating-spatial-views hypothesis. To further strengthen and elaborate on this hypothesis, it is necessary to address three important issues, as listed below.

First, there are concerns that spatial representations used for recognition are not identical to those used for homing. Therefore, the intact recognition observed in the first catch trial, as reported in Chen and Mou (2024), does not necessarily mean that all spatial representations generated by path integration are unimpaired. Spatial representations related to homing might still be impaired due to the suppressed path integration during the outbound phase. Thus, it might be premature to favor the updating-spatial-views hypothesis over the suppression hypothesis. To address this issue, distinguishing between these two hypotheses by using a homing task, rather than a recognition task, is required. A fundamental difference between these two hypotheses concerns whether spatial representations from path integration are impaired during the outbound phase (due to suppressed path integration) or during the homing phase (due to view mismatch causing disorientation). Hence, one primary purpose of this study was to investigate the timing of the homing impairment in the first catch trial.

Second, Chen and Mou (2024) stipulated that the unexpected absence of landmarks in the homing phase of the first catch trial created a huge mismatch between the actual and anticipated views, which disoriented participants. It remains unclear, however, whether such disorientation impaired individuals' estimates of their location, their orientation, or both. Consistently, it is not clear whether the disturbed homing estimates in the first trial of Chen and Mou's (2024) Experiment 1b and Zhao and Warren's (2015a) Experiment 1 were attributed to an impaired position representation, impaired heading representation, or both. Note that the original updating-spatial-views hypothesis did not have a clear prediction on which spatial representations have been disrupted during disorientation. To refine the updating-spatial-views hypothesis, we propose that disorientation might more likely impair orientation representations than position representations. This proposal is based on the insight that disrupting people's orientation representations without disrupting their location representations seems much easier than disrupting people's location representations without disrupting their orientation representations.

Research in human spatial cognition develops a method of impairing people's orientation without disrupting their positions. Disorientation is often required to investigate how people regain their orientation from visual information (e.g., Hermer & Spelke, 1996), integrate orientation cues from path integration and landmarks (e.g., Nardini et al., 2008), and encode objects' locations relative to each other and to an observer's body (e.g., Wang & Spelke, 2000). Across these studies, a common disorientation paradigm involves rapidly spinning participants in place or for an extended period until they lose their sense of orientation. Notably, spinning participants in places disrupts participants' orientation representations while preserving their location representations (Zhang et al., 2020). We are not aware of any studies that have introduced a disorientation paradigm capable of disrupting people's location representations without affecting their orientation representations. Similarity, we cannot conceive of any disorientation method that can disrupt people's location representations without impairing their orientation representations.

Maintaining location representations is often more crucial than maintaining orientation representations in daily life. Our knowledge is typically tied to specific places rather than directions, as we associate particular activities with specific locations—working in the office, sleeping in the bedroom, shopping at the store. Moreover, changing orientation is much faster than changing location. For example, people can rotate 180° in 1.22 seconds at a natural speed, while it takes the same amount of time to cover just 1.7 meters (Khobkhun et al., 2021). Moving 1.7 meters forward changes the angle to an object 1.7 meters away on the sides by 45°, while a 180° rotation shifts the directional relationship by a full 180°.

While we proposed that disturbances in heading estimation are more likely than in position estimation, direct empirical evidence is needed. Therefore, this study also aimed to identify which spatial representation is impaired by the removal of landmarks. Indeed, if we have evidence of a disturbance in heading estimation but not in the position estimation, it should also strengthen the argument that disturbance occurs after, as proposed by the updating-spatial-view hypothesis, rather than during the outbound phase, as proposed by the suppression hypothesis.

After the outbound phase, people's orientation representations can be disturbed without impairing their position representations. Conversely, it is challenging to conceive how, during walking, people's orientation representations could be disturbed while their position representations remain intact.

Third, Chen and Mou (2024) showed that neither recognition of landmarks nor recognition of targets was disrupted in the first catch trial, suggesting that participants updated spatial views of both landmarks and targets. This finding supports the updating-spatial-views hypothesis. However, the updating-spatial-views hypothesis does not specify whether individuals prioritize certain spatial views over others. Addressing this gap would significantly enhance the hypothesis. To revise the hypothesis, we speculate that people should prioritize certain spatial views over others, as it is costly to keep all spatial views in working memory. In particular, participants who exhibited homing disruption in previous studies (Chen & Mou, 2024, Experiment 1b and Zhao & Warren, 2015a, Experiment 1) may have prioritized the spatial views of the landmarks over those of the targets. Consequently, the removal of landmarks created a mismatch with the prioritized spatial view, leading to disorientation. If this speculation is correct, reducing the importance of landmarks might mitigate the homing disruption caused by their unexpected removal. The last main purpose of the current study was to investigate whether diminishing the significance of landmarks can alleviate the disruption.

As an overview of all experiments, Experiment 1 tested which spatial representation (heading or position estimates) was disrupted. Two more objects in addition to the home object were learned in the learning phase and then replaced in the homing phase. Participants' heading and position estimates were calculated based on the replaced locations of multiple objects (Mou & Zhang, 2014; Zhang & Mou, 2017; Zhang et al., 2020). These estimates in the first catch trial would be compared to those in the matched baseline trial to examine the disrupted representations.

Experiments 2 and 3 investigated the timing of disruption. In both experiments, a curtain briefly concealed participants' views before the homing phase. While the curtain was raised to reveal views of an empty ground without landmarks in catch trials of Experiment 2 to create a view mismatch, the curtain remained unraised in Experiment 3 to avoid such a mismatch. A disruption occurring in the outbound phase should be independent of the curtain manipulation and cause homing disruption in both experiments. Conversely, a disruption occurring due to view mismatch during the homing phase should cause homing disruption in Experiment 2 but not in Experiment 3.

Experiments 4 and 5 investigated whether reducing the prevalence of landmarks mitigates homing disruption. In both experiments, participants learned and replaced four additional objects alongside the home object. Furthermore, these four added objects formed a square with the home object at the center. The increased number of objects and the regular layout might increase the importance of the layout of objects and diminish the significance of the three landmarks. If participants prioritized the object layout over the landmarks, they might completely ignore the landmarks. In the second catch trial of Experiment 5, the landmarks were rotated instead of being removed to examine whether people relied on the rotated landmarks for orientation.

2. Experiment 1

The aim of Experiment 1 was to investigate which representation is impaired when stable landmarks unexpectedly disappear. Participants' inability to recall the home location may arise from the loss of position information, heading information, or both. We had three objects as targets in Experiment 1 (see Figure 1c), as previous studies have shown that when participants replace two or more targets, we can calculate their position angular error and heading error, in addition to homing error (Mou & Zhang, 2014; Zhang & Mou, 2017; Zhang et al., 2020). In each trial within an immersive environment, participants first observed three objects including the home object from the starting point (S in Figure 1a) and then proceeded to walk to the home object (O in Figure 1a) (learning phase). Participants then walked an outbound path with two legs (O-T-P) (outbound phase). After completing the outbound phase, participants replaced objects (homing phase).

The presence of visual information was varied across different conditions. In standard trials (see Figure 2), visual landmarks remained consistently visible at fixed locations for the entire duration of the trial. In catch trials (see Figure 2), visual landmarks were shown during the learning and outbound phases but were unexpectedly removed before the homing phase. In baseline trials (see Figure 2), visual landmarks were absent throughout the entire trial. The first nine standard trials preceded the first catch trial to establish participants' anticipation of seeing visual landmarks at fixed locations. The first catch trial was intended to create an unexpected removal of stable landmarks in a familiar environment.

Following the findings of Chen and Mou's (2024) Experiment 1b and Zhao and Warren's (2015) Experiment 1, we expected that the homing errors on the first catch trials would be significantly larger than the homing errors on the first matched baseline trials. For the heading error and position error, as suggested by the revised updating-spatial-views hypothesis, it is much easier to disrupt people's heading than their position representations after walking. Consequently, we predicted that participants' heading errors in the first catch trial would be significantly larger than that in the matched baseline trial whereas their position errors were comparable in these two trials. Alternatively, we do not conceive of any reasons to expect larger position errors but comparable heading errors in the first catch trial. However, the suppress hypothesis predicted larger errors in both heading and position estimates in the first catch trial as the suppressed path integration should have difficulty to update both position and heading representations.

2.1 Method

2.1.1 Participants

The study received approval from the Ethics Committee of the University of Alberta. Thirty-two university students (16 females, 16 males) with normal or corrected-to-normal vision and be able to walk independently participated as partial fulfillment of a requirement for their introductory psychology courses. All participants provided consent to participate in this experiment. In this and following experiments, participants only participated one experiment in our lab.

Given the effect size (Cohen's *dz* = 0.524) observed for the difference between the first catch and baseline trials in Experiment 1b of Chen and Mou (2024), a sample size of 32 participants would provide a power of 0.8189 to detect a significant difference in homing errors between the first catch and baseline trials, using a two-tailed paired t-test with an alpha level of .05.

2.1.2 Material and Design

The experiment was identical to Experiment 1b of Chen and Mou (2024), except that we used 3 objects as targets. The real experiment room was roughly 4.0 x 4.0 meters large. An immersive virtual environment was created by Vizard software (WorldViz, Santa Barbara, CA) and presented to participants by using a head-mounted display (HMD, Oculus Rift, Oculus VR, LLC., Irvine, CA). An InterSense IS-900 motion tracking system (InterSense, Inc., Massachusetts) was used to track head motion.

Participants used a virtual stick, which they maneuvered through head movements, to point to the locations of targets. The virtual stick originated from a head motion tracker and aligned with the participants' head-facing direction, intersecting with the ground (an open grass field) to mark the response location. The virtual stick was 100 meters long to encompass all possible object locations within the current project. It was visible only when participants needed to reposition objects. Specifically, a probed object appeared to float at the right corner of their field of vision, and the virtual stick, originating from and aligning with their head, would appear. Participants pressed a button on a hand-held remote to confirm the intersection between the virtual stick and the ground as the response location of the probed object. Once participants confirmed their response by pressing the button, the virtual stick vanished to avoid obstructing their view.

Participants physically walked and made turns to navigate within the real lab room, even though they never actually saw the room itself. In each trial, a starting point (S in Figure 1a) was indicated by a red arrow on the ground, and three 2-meter-tall colored poles were used to indicate the origin, turning point, and testing position (i.e., O-T-P, see Figure 1a). Each colored pole was presented one at a time in a fixed order (i.e., red - red - green) (see an example of a red pole with 3 objects from bird’s-view in Figure 1c). Twelve different paths were used in this experiment, all with different origins (O in Figure 1b) but sharing the same turning point (T in Figure 1b) and testing position (P in Figure 1b). The lengths of the origin to the turning point (O-T) and turning point to the testing position (T-P) were fixed at 1.8 meters and 1.2 meters, respectively. The 12 possible origins (O, see Figure 1b) were positioned on a circle centered on the turning point (T) with a radius of 1.8 meters. The turning angle varied between 35° and 110° clockwise or counter-clockwise, divided into 15° increments. Across trials, the start location (S) was fixed and marked by a red arrow on the ground, which pointed to the home (i.e., the first red pole) of each specific trial (see Figure 1c).

Three different 2-meter-tall towers, resembling the Eiffel tower, Big Ben, and CN Tower, served as landmarks (in Figure 1c). These towers positioned 5 meters from the testing position (P in Figure 1a). The middle tower aligned with the start point (S) and the testing position (P) along the same axis. The remaining two towers were spaced 45° apart from the middle tower. These tower placements remained consistent throughout the experiment. Three different objects (i.e., a clock, a ball and a brush) were used as targets. One of them was placed at the home location (O). The other two objects were placed 1.41 meters from the home in the direction of 45° clockwise or counter-clockwise relative to the participants' initial facing direction (i.e., from S to O) (see the red arrow in Figure 1c). Across participants, three objects randomly appeared at the three locations whereas within each participant, the association between objects and locations was fixed across trials.

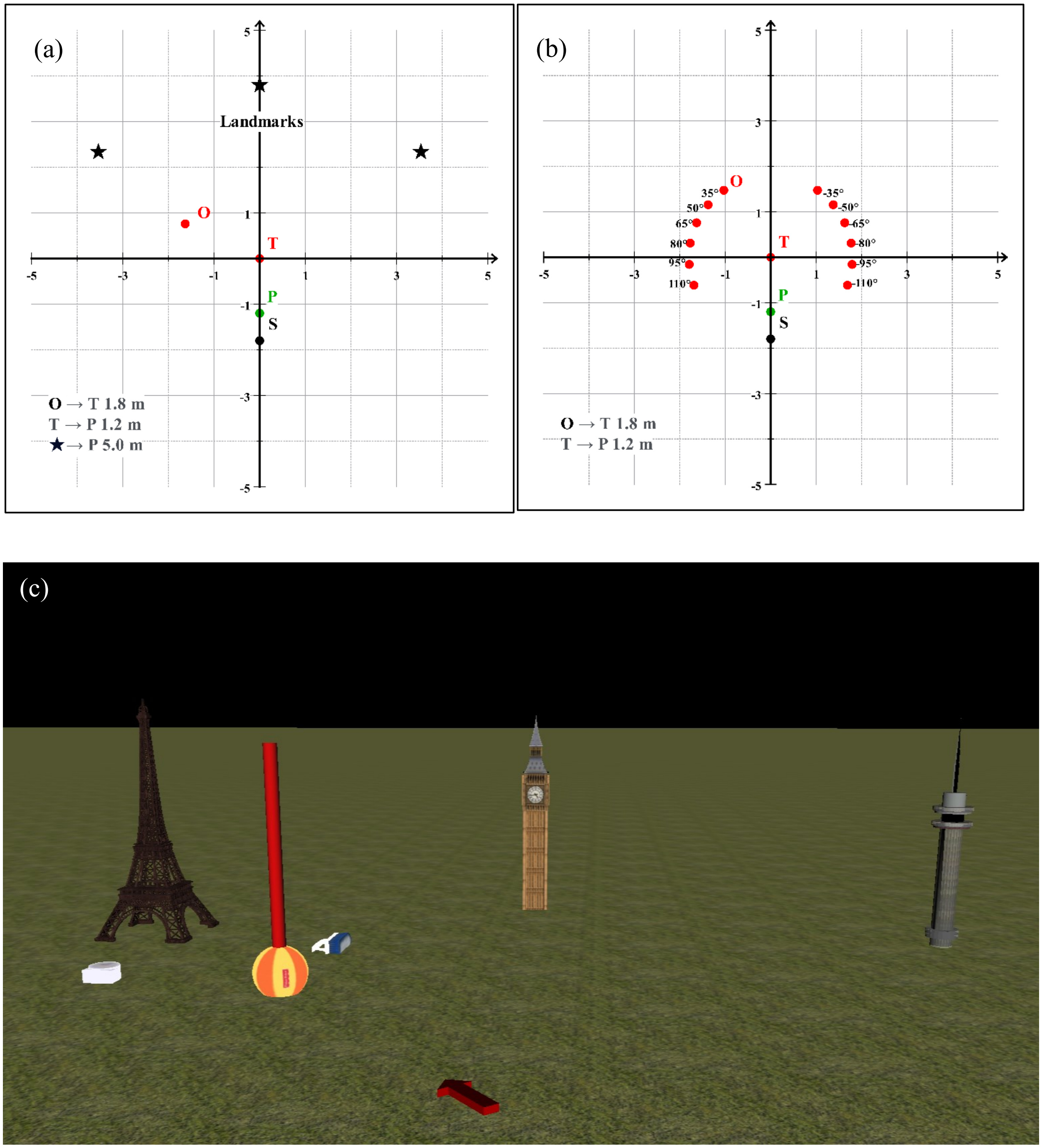


Figure 1. *(a) Schematic of the experimental setup in Experiment 1. The stars represent the locations of three landmarks. S represents the start location, O represents the home location, T represents the turning point, and P represents the*

Accepted in Journal of Experimental Psychology: Learning, Memory, and Cognition

testing location. The O-T-P segment constitutes the outbound path. (b) Twelve possible home locations, indicated by the red dots with their corresponding degrees, and the associated outbound paths. The turning angles of the outbound paths varied between 35° and 110°, in 15° increments (positive values indicate a clockwise turning direction). (c) A screenshot of a sample trial in the virtual environment, featuring three visual landmarks: the first red pole (indicating the home object's location, O), the possible location of the object array in Experiment 1, and the start location (S), marked by a red arrow to indicate the initial facing direction.

In the standard trials, landmarks remained visible and fixed throughout (see Figure 2), and participants were only required to point to the home object during the homing phase. In catch trials, landmarks were visible only before the homing phase, while in baseline trials, no visual landmarks were present at any point. During catch and baseline trials, participants first indicated the location of the home object, followed by the other two objects in random order. A total of 24 trials were conducted: the first nine were standard trials (referred to as familiarity trials in the results section), followed by a catch trial, another nine standard trials, and then a second catch trial. The final four trials were baseline trials, with the first two being unmatched baseline trials and the last two being matched baseline trials.

For each participant, nine out of twelve possible paths were randomly selected and assigned to the standard trials. The two paths used in the catch and matched baseline trials were randomly chosen from the remaining three unselected paths. The paths in the catch and matched baseline trials were paired according to their trial order (e.g., the first catch trial used the same path as the first baseline trial). The two paths used in the unmatched baseline trials were randomly chosen from those for the standard trials.

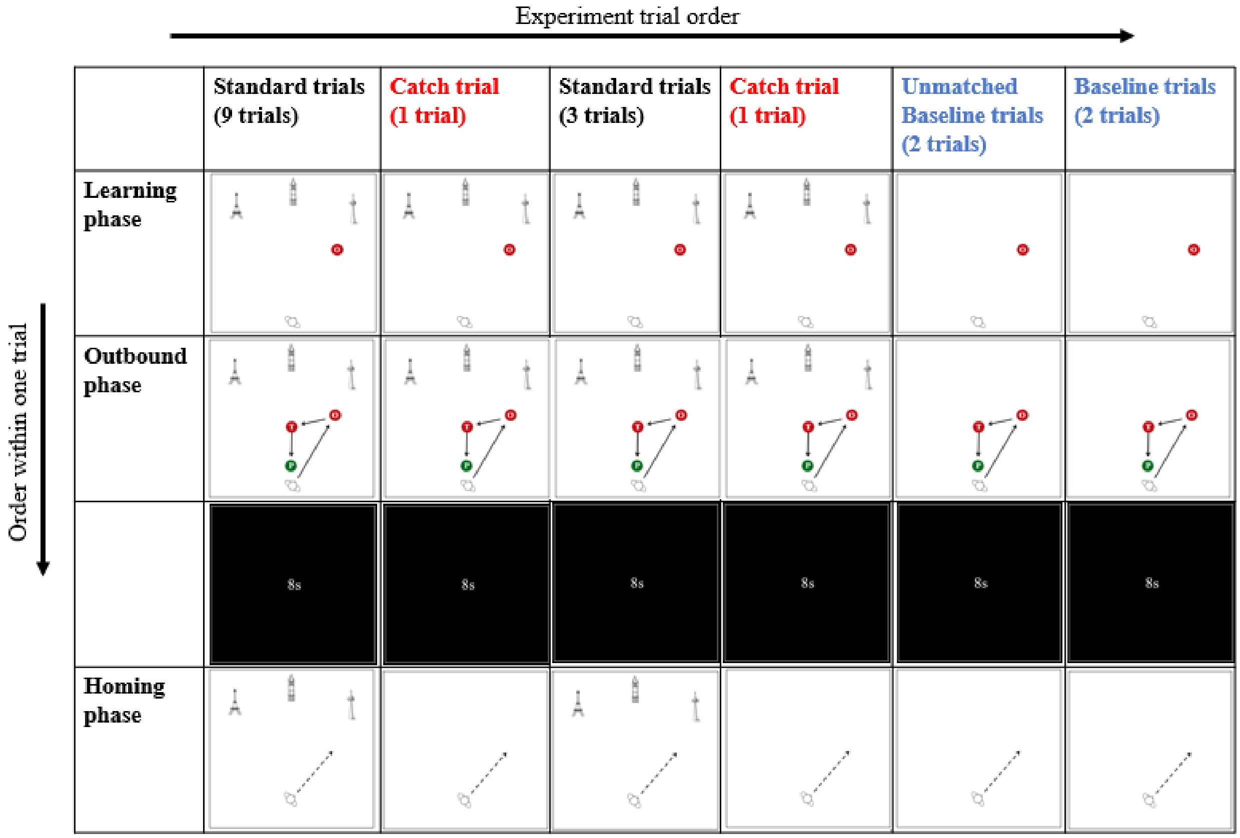


Figure 2. The timeline of the trial in Experiment 1 for all kinds of trial conditions.

While for standard trials, we measured participants' estimates of home locations, for catch and baseline trials, we measured participants' replaced locations of all three objects (see the replaced objects in Figure 3a). We calculated participants' estimates of their heading and position using a bi-dimensional regression from the three correct and replaced object locations in the homing phase of each catch or baseline trial (Zhang et al., 2020). Accordingly, the dependent variable was only the absolute homing angular error. The homing angular error refers to the angular disparity (θ in Figure 3b) between the correct homing direction (from P to O, see Figure 3b) and the participants' response of the homing direction (from P to O') in standard trials. For the catch and baseline trials, the dependent variables were, in addition to the absolute homing angular error, the absolute heading error and the absolute position angular error. The heading error refers to the angular difference (η in Figure 3b) between participants' correct heading (h) and participants' estimated heading (h'). The position angular error refers to the angular difference (π in Figure 3b) between the direction of participants' correct position relative to the home (from O to P) and the direction of participants' estimated position relative to the home (from O to P').

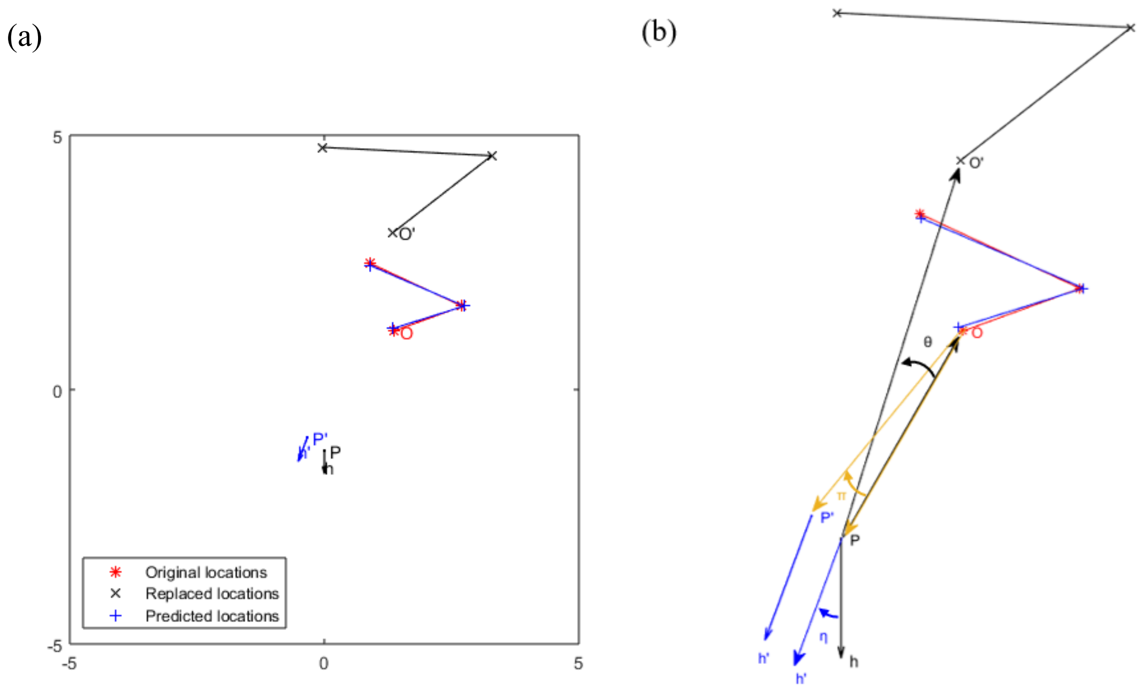


Figure 3. *(a) A sample of a participant' responses were calculated with a bi-dimensional regression between the replaced and original locations. (b) A graph illustrating the homing angular error, the angular disparity (θ) between the correct homing direction (from P to O) and the participant's response of the homing direction (from P to O'); the heading error, the angular difference (η) between participant's correct heading (h) and participant's estimated heading (h'); the position angular error, the angular difference (π) between the direction of participant's correct position relative to the home (from O to P) and the direction of participant's estimated position relative to the home (from O to P'). Note that all errors (θ, η, and π) are the estimated values minus the correct values, e.g. $\eta = h' - h$. Clockwise is the positive direction.*

Accepted in Journal of Experimental Psychology: Learning, Memory, and Cognition

2.1.3 Procedure

Before the experiment, participants read and signed the consent form and received instructions in a waiting room separate from the virtual environment room. An experimenter then guided them to the virtual environment room. Participants kept their eyes closed until the experimenter placed the HMD on their heads. To minimize any orientation cues from the surrounding environment, white noise was played through the HMD earphones at a volume that allowed participants to still hear the experimenter's voice clearly. Participants received instructions displayed on the HMD and, when necessary, from the experimenter. Following the instructions on the HMD, they were directed to look for a red arrow on the ground (at S in Figure 1a) (e.g., "You will see an arrow on the ground."). They were then asked to walk toward the arrow and align themselves with its direction ("Please walk to the arrow and turn to align with the arrow.") to begin each trial.

As the start of the learning phase, the first red pole (at O in Figure 1a) appeared in front of the participants ("Please find a red pole in front of you."), along with the three towers and three objects ("You will see 3 objects around the red pole."). Participants were given a few seconds (i.e., 60 seconds for the first trial, 15 seconds for all the following trials) to memorize the location of the object array ("You have a few seconds to remember the location of the object array."). After that, the object array disappeared, the virtual stick appeared along with one probed object. Participants were instructed to place the object back to its original location with the red pole there. The experimenter delivered instructions to participants in this part in order to make sure participants fully understood how to use the virtual stick. After each replacement, the correct location of the probed object was presented as feedback. After replacement and feedback of all three objects, participants were then instructed to walk towards the first red pole ("Please walk to the red pole."). Once participants reached it, the first red pole vanished. The learning phase of this trial ended.

As a start of the outbound phase, one second red pole (at T in Figure 1a) emerged, and participants were asked to face and walk towards it ("Please turn RIGHT/LEFT to walk to the 2nd red pole."). The instructions always indicated the turning direction with the smaller turning angle for each outbound path. Participants were instructed to turn their body slowly until they could see the second red pole and then walk towards it. When they reached it, the second red pole disappeared. The same process was repeated to reach the green pole (P, "Please turn RIGHT/LEFT to the green pole."). When the participants reached the green pole, their view of the virtual environment was obscured for 8 seconds.

The testing phase started after the brief view obscuration. Participants were instructed ("Please point to the location of the object at the original position.") to turn their body around and indicate the original location of the object using the virtual stick with one probed object emerged. For standard trials, participants were asked to replace the home object only, while for the catch and baseline trials, they were asked to replace the home object first and then the other two objects. Specifically, the virtual eye stick appeared, and participants were asked to move their head to align the virtual eye stick with the location of their response, then press a button on a hand-held remote to confirm their responses. After confirmation, the location of their response was recorded. All visual elements, except for the grass field, were then removed, and participants were guided to a random location with their eyes closed. When they opened their eyes, the red arrow reappeared to indicate the start position (S), and the next trial began.

The entire experiment lasted less than one hour, and participants were allowed to take breaks if they wished. If such cases, experimenters removed the HMD while participants closed their eyes and led them outside the experiment room for breaks, although this occurrence was rare.

2.1.4 Data analysis

For each trial, we computed the absolute homing error. The mean absolute homing error was calculated for each participant in every trial condition. We compared the mean absolute homing error across different conditions using repeated-measures ANOVAs with one within-participant variable of trial type (Database: https://doi.org/10.7939/r3-effv-6j83).

For the catch and baseline trials, we also calculated the absolute heading error and absolute position error (see Figure 3). Given our primary interest in comparing performance between catch trials and their corresponding baseline trials, particularly the first catch and matched baseline trials, we conducted 2-tailed paired t-tests to compare three kinds of errors in the matched catch and baseline trials.

To evaluate the presence of any null effect, we also computed the Bayes factor favoring the null effect over the alternative effect (BF01) using JASP (JASP Team, 2024. JASP (Version 0.18.3) [Windows 11]).

2.2 Results

To distinguish the first nine standard trials from the remaining nine standard trials, we labeled the initial nine standard trials as familiarity trials and the other nine as standard trials.

Figure 4a displays the overall mean absolute homing error for each condition. There was no significant difference in the mean absolute homing error between the familiarity trials and standard trials, $t(31) = 1.122$, $p = .270$, Cohen's $dz = 0.198$, $BF_{01} = 2.979$. Similarly, the mean absolute homing error did not significantly differ between the unmatched baseline trials and the

Accepted in Journal of Experimental Psychology: Learning, Memory, and Cognition

matched baseline trials, $t(31) = -1.108$, $p = .276$, Cohen's $dz = -0.196$, $BF_{01} = 3.021$. Consequently, we compared the mean absolute error among the all 18 standard trials (9 familiarity trials and 9 standard trials), the catch trials, and all 4 baseline trials (2 unmatched baseline trials and 2 matched baseline trials). The main effect remained significant after the Huynh-Feldt correction ($\varepsilon = .711$), $F(1.422, 44.086) = 14.994$, $p < .001$, $MSE = 6764.374$, $\eta_p^2 = .326$. Post-hoc testing using Bonferroni correction revealed the following significant differences: the homing error was significantly smaller in the standard trial condition than in the catch trial condition (mean difference = -24.503, $p < .001$, Cohen's $dz = -1.217$) and baseline trial condition (mean difference = -13.052, $p = .015$, Cohen's $dz = -0.648$). In addition, the homing error in the catch trial condition was significantly larger than in the baseline trials condition (mean difference = 11.450, $p = .039$, Cohen's $dz = 0.569$).

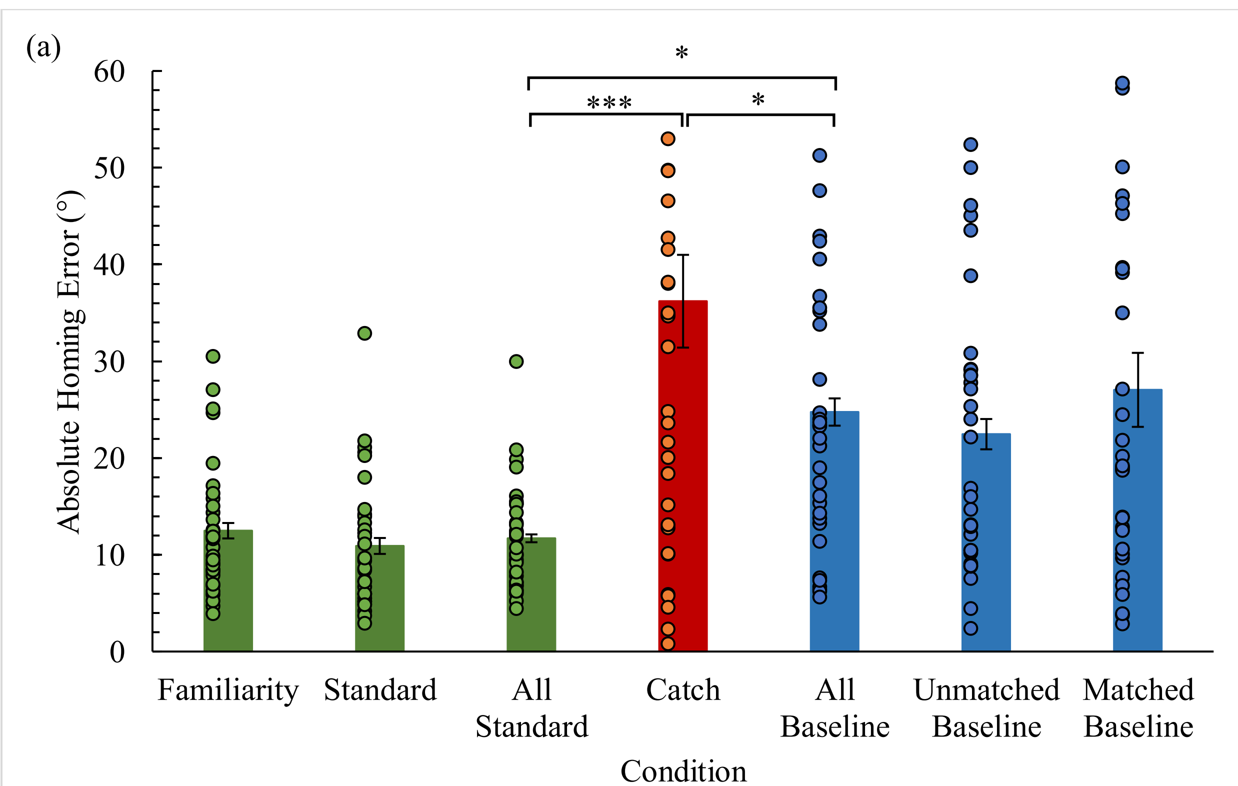
Figure 4b depicts the absolute homing error for each catch trial and its matched baseline trials. A repeated measures ANOVA was conducted to examine the effect of the trial type (catch vs. baseline) and trial sequence (the first trial vs. the second trial) on homing error. There was no significant main effect of trial type, $F(1, 31) = 2.622$, $p = .115$, $\eta_p^2 = .078$, nor was there a significant main effect of trial sequence, $F(1, 31) = 1.444$, $p = .239$, $\eta_p^2 = .045$. The interaction between trial type and trial sequence was also not significant, $F(1, 31) = 2.538$, $p = .121$, $\eta_p^2 = .076$.

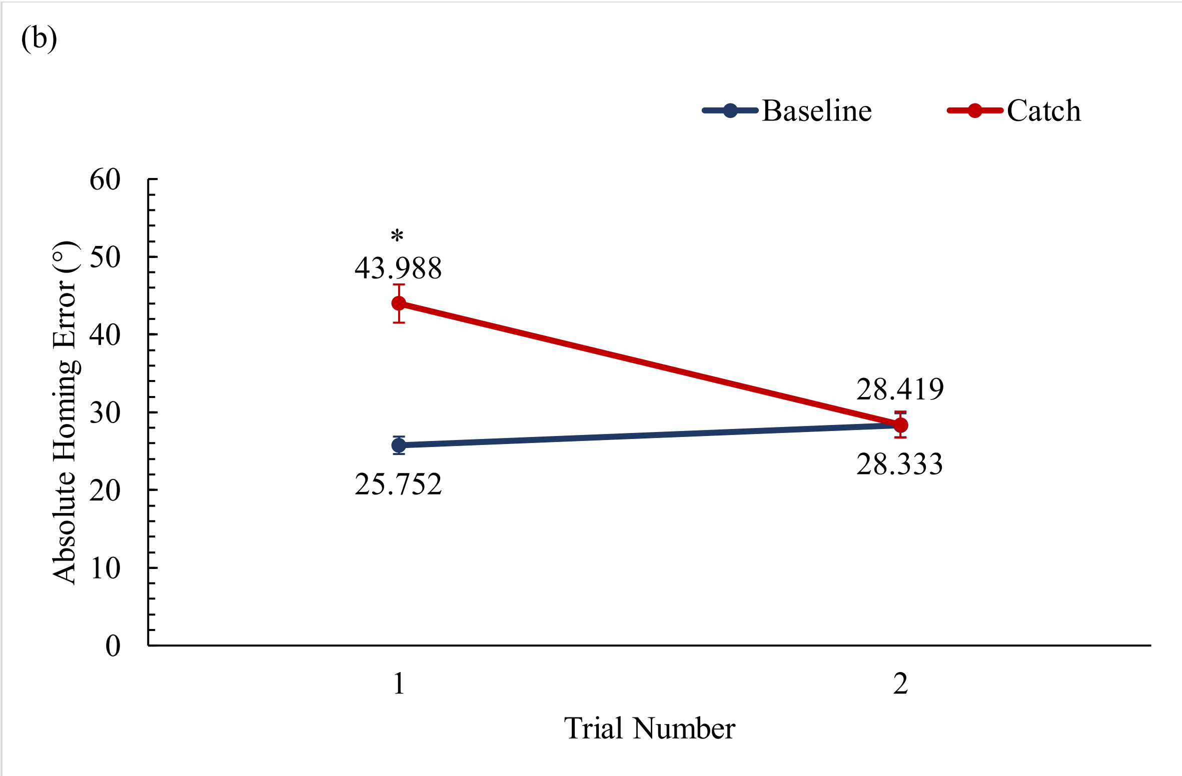
The failure to detect a significant interaction, which was observed in all subsequent experiments except for Experiment 5, might be due to a lack of statistical power. Only the comparison between the first catch and baseline trials was relevant for distinguishing between the two theoretical hypotheses of this project. The comparison between the second catch and baseline trials was not relevant for distinguishing between the two theoretical hypotheses as both hypotheses would predict no difference between these two trials. Therefore, the power analysis conducted prior to the current experiments was based on the difference between the first catch and baseline trials in Experiment 1b of Chen and Mou (2024), rather than on detecting an interaction. Detecting a significant interaction, which would involve a difference between the first catch and baseline trials but no difference between the second catch and baseline trials, would require approximately double the number of participants to achieve the same power as detecting a significant difference between the first catch and baseline trials. Specifically, the prior Cohen's dz for the difference between the first catch and baseline trials (i.e. $dz = \frac{\mathrm{C1-B1}}{\sqrt{2MSE}}$) is $\sqrt{2}$ of the prior Cohen's *dz* for the interaction (i.e., $dz = \frac{\mathrm{(C1-B1)-(C2-B2)}}{\sqrt{4MSE}}$, $with\ \mathrm{C2} - \mathrm{B2} = 0$). Based on the prior Cohen's *dz* of 0.524 for the difference between the first catch and baseline trials, we calculated a prior Cohen's *dz* of 0.371 for the interaction. A sample size of 32 participants, which was used in the current experiment, would provide a power of 0.5283 to detect a significant interaction, using a two-tailed paired t-test with an alpha level of .05. This is much lower than the power of 0.8189 to detect a significant difference between the first catch and baseline trials. Additionally, a sample size of 62 participants would be needed to achieve a power of 0.8189 to detect a significant interaction.

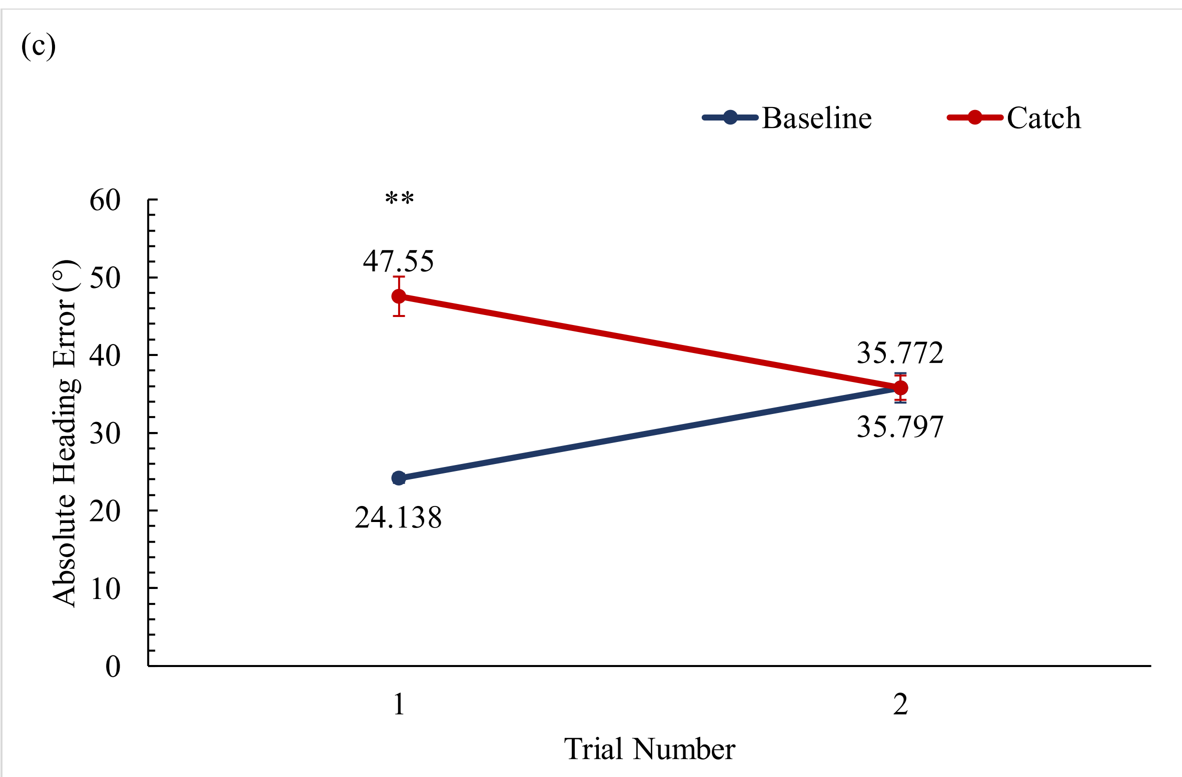
Hence, in this and following experiments, we conducted *planned* paired t-tests to access the differences between the first catch trial and first baseline trial, as well as between the second catch trial and second baseline trial regardless of whether there was a significant interaction. The homing error showed a significant increase in the first catch trial compared to the first matched baseline trial, $t(31) = 2.189$, $p = .036$, Cohen's $dz = 0.387$, $BF_{01} = 0.662$. However, this notable difference vanished in the second catch trial and its matched baseline trial, $t(31) = 0.011$, $p = .991$, Cohen's $dz = 0.002$, $BF_{01} = 5.295$.

Figure 4c shows the absolute heading error for each catch trial and its matched baseline trials. Similar with the pattern in the absolute homing error, the heading error showed a significant increase in the first catch trial compared to the corresponding baseline trial, $t(31) = 2.828$, $p = .008$, Cohen's $dz = 0.500$, $BF_{01} = 0.190$. However, the heading error in the second catch trial return to the baseline level, $t(31) = 0.003$, $p = .998$, Cohen's $dz = 5.151\text{x}10^{-4}$, $BF_{01} = 5.295$.

Figure 4d demonstrates the absolute position error for each catch trial and its matched baseline trials. The heading error in the first catch trial is comparable to its matched baseline trial, $t(31) = 0.507$, $p = .616$, Cohen's $dz = 0.090$, $BF_{01} = 4.701$. However, the position error showed a significant increase in the second catch trial compared to the second matched baseline trial, $t(31) = -2.267$, $p = .031$, Cohen's $dz = -0.401$, $BF_{01} = 0.575$.




(b)
Baseline
Catch
Absolute Homing Error (°)
60
50
40
30
20
10
0
*
43.988
28.419
28.333
25.752
1
2
Trial Number


(c)
Baseline
Catch
Absolute Heading Error (°)
60
50
40
30
20
10
0
**
47.55
35.772
35.797
24.138
1
2
Trial Number

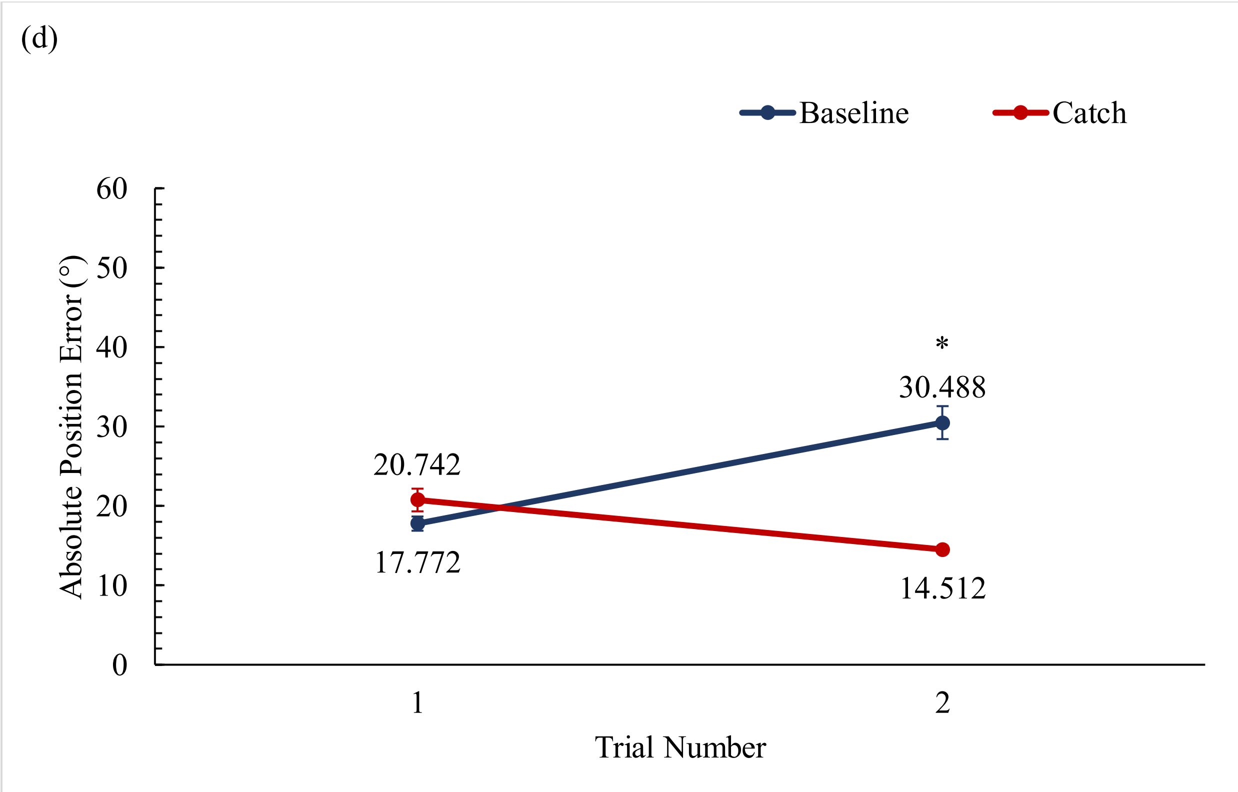


Figure 4. *(a) Absolute homing error for each condition in Experiment 1. Each dot represents one participant. (b) Absolute homing error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 2nd) in Experiment 1. The error bar was calculated by removing the error due to individual differences from the standard error of each trial. (c) Absolute heading error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 2nd) in Experiment 1. The error bar was calculated by removing the error due to individual differences from the standard error of each trial. (d) Absolute position error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 2nd) in Experiment 1. The error bar was calculated by removing the error due to individual differences from the standard error of each trial.*

2.3 Discussion

Experiment 1 replicated the main findings of Experiment 1b of Chen and Mou (2024) and Experiment 1 of Zhao and Warren (2015a), indicating that homing error was larger for the first catch trial than for the first matched baseline trial. The non-standardized difference was 18°, aligning closely with the disparity observed in Chen and Mou (2024) (i.e., in Experiment 1b, the difference was 20°). Thus, we have replicated the main finding of previous experiments.

More important, heading error was significantly larger in the first catch trial than for the first matched baseline trial. The non-standardized difference was 23°, which is also aligning closely with the disparity observed in homing errors. In contrast, the position angular error did not show any difference in the first catch and matched baseline trials. Therefore, we can conclude that the unexpected removal of visual landmarks in a familiar environment disrupts navigators' representations of heading but not their representations of position. The updating-spatial-views hypothesis could be revised to suggest that participants update their spatial views of environments using path integration in familiar settings, and the absence of stable visual landmarks disrupts orientation but not position representations.

This result also suggested that the disruption of homing in the first catch trial might have occurred during the homing phase as proposed by the updating-spatial-views hypothesis rather than the outbound phase as proposed by the suppression hypothesis. If updating the homing vector had occurred in the outbound phase due to suppression of path integration, the suppression of path integration would disrupt participants' position estimate as well as heading estimates.

However, spatial memory and spatial updating of three objects in Experiment 1 could be different from spatial memory and spatial updating of the home only in Experiment 1b of Chen and Mou (2024) and Experiment 1 of Zhao and Warren (2015). In Experiments 2 and 3 of the current study, we further investigated when this disruption occurred to distinguish between the updating-spatial-views hypothesis and the suppression hypothesis by employing the home object only. Different from Experiment 1, where the HMD was turned to black to block any visual information during the 8-second break between the outbound phase and homing phase, Experiments 2 and 3 used a curtain to cover participants' view. In Experiment 2, consistent across all types of trial conditions, curtain was first lowered to occlude the scene and then raised to reveal the scene. The landmarks were removed to create mismatched views in catch trials. Conversely, in Experiment 3, the curtain was lowered and then remained in place for both catch trials and baseline trials, blocking the view of the landmarks to prevent the creation of mismatched views.

The suppression hypothesis predicts impairment in both experiments, as it suggests that path integration is suppressed in familiar environments. Therefore, without the visibility of landmarks, participants would have difficulty retrieving the original location of home, regardless of how we manipulated the disappearance of the landmarks. However, the updating-spatial-views hypothesis predicts impairment in Experiment 2 but not in Experiment 3, since there is a mismatched view in Experiment 2 due to the removal of landmarks, while in Experiment 3, the blocking of landmarks does not create a mismatched view.

3. Experiment 2

Experiment 2 used the home object only. In addition, a curtain was introduced to obscure the participants' view of the environment during the 8-second view occlusion, similar to the black screen used in Experiment 1. The curtain was lowered to block the view and then raised after 8 seconds, allowing participants to see the environment again. The curtain in Experiment 2 essentially replicated the occlusion function of the black screen from Experiment 1, serving the same purpose of temporarily preventing visual access to the environment. During the catch trials, the landmarks were removed, and participants had to rely on the spatial representations from path integration to complete the homing phase. Both the suppression and updating-spatial-views hypotheses predicted that homing would be disrupted during the first catch trial, consistent with previous findings from Chen and Mou (2024) and Zhao and Warren (2015).

The primary reason for using a curtain in Experiment 2, as opposed to a black screen, was to establish a baseline for Experiment 3, where the curtain remained lowered after the 8-second period to block the participants' view of the environment. This setup allowed for a contrast between the suppression and updating-spatial-views hypotheses (see detailed rationales in Experiment 3).

3.1 Method

3.1.1 Participants

Thirty-two university students (16 females, 16 males) with normal or corrected-to-normal vision and be able to walk independently participated as partial fulfillment of a requirement for their introductory psychology courses.

3.1.2 Material, Design, and Procedure

Experiment 2 was similar to Experiment 1 with the following changes. 1. Instead of turning the HMD to black to obscure participants' view for 8 s between the outbound phase and homing phase, we used a circular curtain to obscure the view. 2. Experiment 2 featured fewer trials, compared to 24 trials in Experiment 1, 18 trials were used in Experiment 2. Only the home object was used as the target, specifically a ball, instead of three objects in Experiment 1.

During the 8-second break between the outbound phase and response phase, participants were surrounded by a black circular curtain which is 3.7 meters high and 4 meters in radius, taking the participant's response location (P) as the center. Given that the towers were 2 meters high and situated 5 meters away from the participants' response location (P), the curtain when being lowered could conceal the towers. The curtain's raise and lower time was less than 1 second.

In total, there were 18 trials: the first nine were standard trials (also termed familiarity trials in the result section), followed by the first catch trial, three more standard trials, and the second catch trial. The final four trials were baseline trials, with the first two categorized as unmatched baseline trials and the latter two categorized as matched baseline trials.

A ball was used as target in Experiment 2. Different from Experiment 1, participants did not have a replacement-feedback part during learning phase. Instead, participants were given 10 seconds to remember the location of the ball as in Experiment 1b of Chen and Mou (2024).

3.2 Results

The figure 5a displays the overall mean absolute homing error for each condition. There was no significant difference in the mean absolute homing error between the familiarity trials and standard trials, $t(31) = -0.218$, $p = .829$, Cohen's $dz = -0.039$, $BF_{01} = 5.179$. Similarly, the mean absolute homing error did not significantly differ between the unmatched baseline trials and the matched baseline trials, $t(31) = 1.023$, $p = .314$, Cohen's $dz = 0.181$, $BF_{01} = 3.277$. Consequently, we compared the mean absolute error among the all 12 standard trials (9 familiarity trials and 3 standard trials), the catch trials, and all 4 baseline trials (2 unmatched baseline trials and 2 matched baseline trials). The main effect remained significant after the Huynh-Feldt correction ($\varepsilon = .736$), $F(1.472, 45.624) = 12.636$, $p < .001$, $MSE = 3601.582$, η_p^2

= .290. Post-hoc testing using Bonferroni correction revealed the following significant differences: the homing error was significantly smaller in the standard trial condition than in the catch trial condition (mean difference = -18.201, $p < .001$, Cohen's dz = -1.008) and baseline trial condition (mean difference = -9.130, $p = .043$, Cohen's dz = -0.506). In addition, the homing error in the catch trial condition was significantly larger than in the baseline trials condition (mean difference = 9.071, $p = .045$, Cohen's dz = 0.502).

The figure 5b depicts the absolute homing error for each catch trial and its matched baseline trials. A repeated measures ANOVA was performed to assess the impact of trial type (catch vs. baseline) and trial sequence (first trial vs. second trial) on homing error. The analysis revealed a significant main effect of trial type, $F(1, 31) = 8.703$, $p = .006$, $\eta_p^2 = .219$, indicating a significant difference in homing error between the catch trial and baseline trial conditions. However, the main effect of trial sequence was not significant, $F(1, 31) = 1.175$, $p = .287$, $\eta_p^2 = .037$, and the interaction between trial type and trial sequence was also non-significant, $F(1, 31) = 1.277$, $p = .267$, $\eta_p^2 = .040$.

Planned paired t-tests were conducted to compare the first catch trial with the first baseline trial, as well as the second catch trial with the second baseline trial. Initially, the homing error showed a significant increase in the first catch trial compared to the first matched baseline trial, $t(31) = 2.120$, $p = .042$, Cohen's dz = 0.375, BF_{01} = 0.747. However, this notable difference vanished in the second catch trial and matched baseline trial, $t(31) = 0.824$, $p = .416$, Cohen's dz = 0.146, BF_{01} = 3.872.

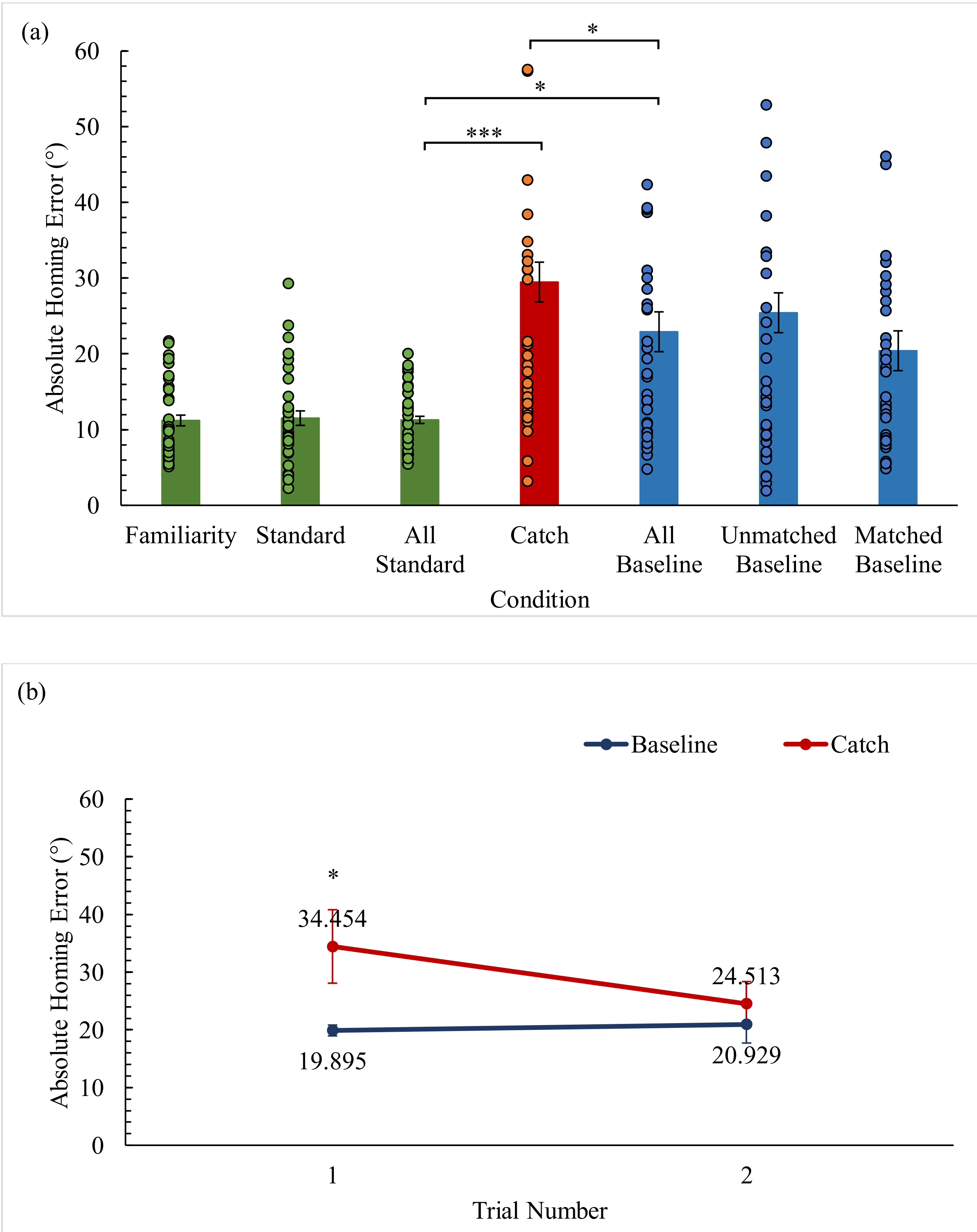

(a)
*
*
***
60
50
40
30
20
10
0
Absolute Homing Error (°)
Familiarity
Standard
All Standard
Catch
All Baseline
Unmatched Baseline
Matched Baseline
Condition
(b)
Baseline
Catch
60
50
40
30
20
10
0
Absolute Homing Error (°)
*
34.454
19.895
24.513
20.929
1
2
Trial Number

Figure 5. (a) Absolute homing error for each condition in Experiment 2. Each dot represents one participant. (b) Absolute homing error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 2nd) in Experiment 2. The error bar was calculated by removing the error due to individual differences from the standard error of each trial.

3.3 Discussion

Experiment 2 replicated the main findings of Experiment 1b of Chen and Mou (2024), demonstrating that the homing error was larger for the first catch trial than for the first matched baseline trial when the stable visual landmarks were removed in a familiar environment.

In Experiments 2, we used curtains, while in Experiment 1, we did not. Specifically, after participants completed the outbound path, a curtain (in Experiment 2) or a black screen (in Experiment 1) appeared to block their view of the environment for eight seconds. After this eight-second occlusion, participants could see the environment again (an open grass field with landmarks removed) in both experiments. The use of a curtain or not did not affect the impairment in homing performance. Homing performance was disrupted in both experiments. Therefore, a visual transient involving either a very rapid occlusion with a black screen or a gradual occlusion with a curtain seems to have similar effects (i.e., briefly blocking the view).

4. Experiment 3

Experiment 3 was identical to Experiment 2, except for the manipulation of the curtain. In Experiment 3, the black curtain remained unraised after the 8-second break and throughout the homing phase. Previous studies have showed that spatial view cells still fired when a curtain blocked monkeys' view of the environment (Rolls, 1999). Inspired by this, the updating-spatial-views hypothesis posits that there were no disparities between the predicted and actual views of landmarks, as participants likely retained their mental representation of the visual landmarks behind the curtain. Therefore, this hypothesis predicts that the homing error in the first catch trial would be statistically equivalent to the homing error in the first baseline trial, with this pattern continuing into the second catch trial and the matched baseline trial. However, the suppression hypothesis predicts impairment in the first catch trial as suppression of path integration, which occurred in the outbound phase, should still occur independent of the unraised curtain in the homing phase.

4.1 Method

4.1.1 Participants

Thirty-two university students (16 females, 16 males) with normal or corrected-to-normal vision and be able to walk independently participated as partial fulfillment of a requirement for their introductory psychology courses.

4.1.2 Materials, design, and procedures

Experiment 3 was identical to Experiment 2 with the modification of the catch trial condition and baseline trial condition. In both catch trials and baseline trials, the curtain remained unraised after the 8-second break and throughout the homing phase.

4.2 Results

The figure 6a displays the overall mean absolute homing error for each condition. There was a significant difference in the mean absolute homing error between the familiarity trials and standard trials, $t(31) = 2.896$, $p = .007$, Cohen's $dz = 0.512$, $BF_{01} = 0.165$. However, the mean absolute homing error did not significantly differ between the unmatched baseline trials and the matched baseline trials, $t(31) = 0.774$, $p = .445$, Cohen's $dz = 0.137$, $BF_{01} = 4.016$. Consequently, we compared the mean absolute error among the 3 standard trials between the two catch trials, the catch trials, and all 4 baseline trials (2 unmatched baseline trials and 2 matched baseline trials). The main effect remained significant after the Huynh-Feldt correction ($\varepsilon = 0.860$), $F(1.719, 53.301) = 6.239$, $p = .005$, $MSE = 2079.223$, $\eta_p^2 = .168$. Post-hoc testing using Bonferroni correction revealed the following significant differences: the homing error was significantly smaller in the standard trial condition than in the catch trial condition (mean

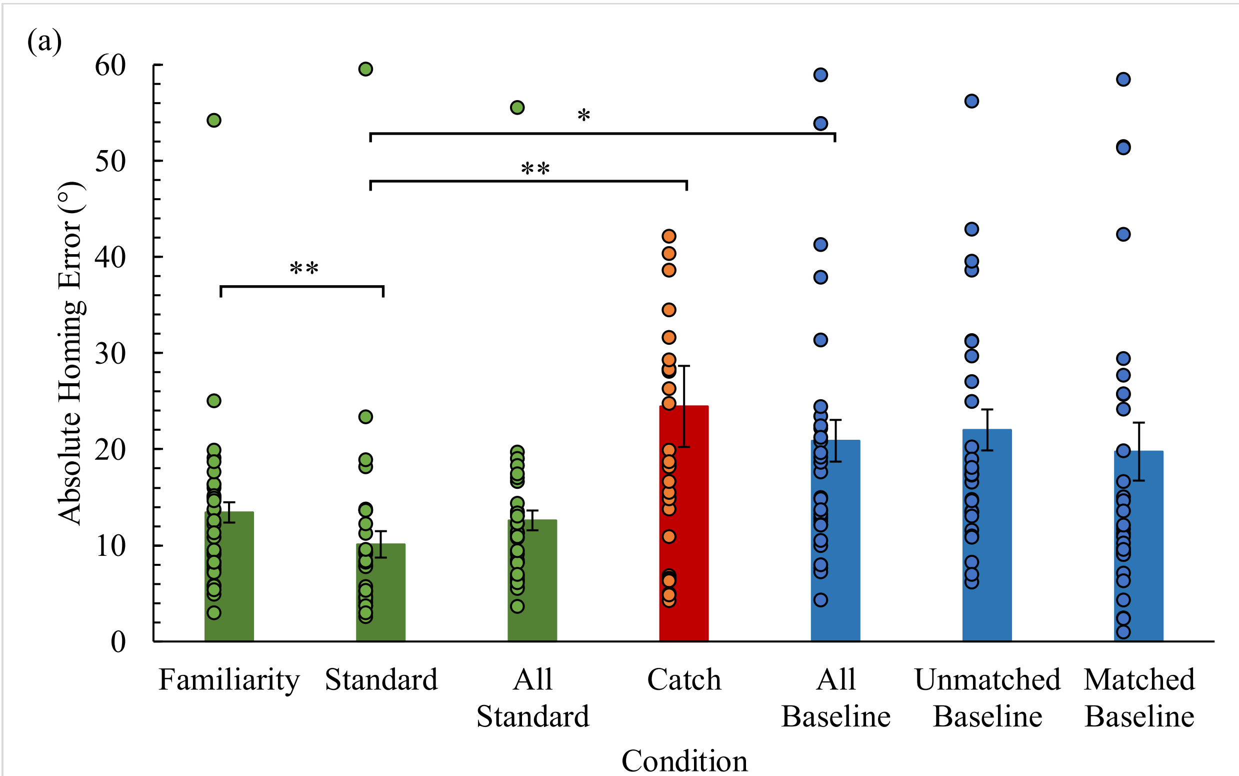
Accepted in Journal of Experimental Psychology: Learning, Memory, and Cognition

difference = -14.358, p = 0.004, Cohen's dz = -0.821) and baseline trial condition (mean difference = -10.780, p = .040, Cohen's dz = -0.616). Moreover, the homing error was comparable in the catch trial condition and baseline trial condition (mean difference = 3.578, p = 1.000, Cohen's dz = 0.205).

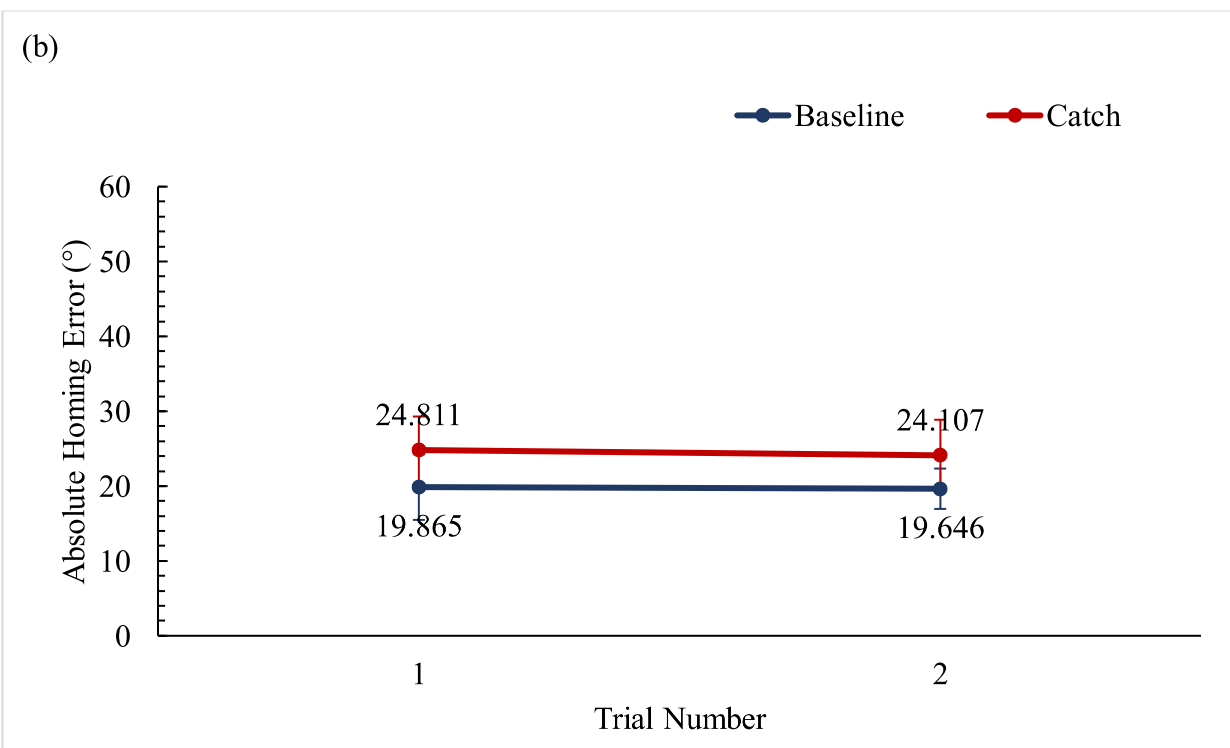
The figure 6b depicts the absolute homing error for each catch trial and its matched baseline trials. A repeated measures ANOVA was performed to investigate the impact of trial type (catch vs. baseline) and trial sequence (first trial vs. second trial) on homing error. The analysis revealed no significant main effect of trial type, $F(1, 31) = 0.908$, $p = .348$, $\eta_p^2 = .028$, and no significant main effect of trial sequence, $F(1, 31) = 0.016$, $p = .900$, $\eta_p^2 = 5.211 \times 10^{-4}$. Additionally, the interaction between trial type and trial sequence was not significant, $F(1, 31) = 0.004$, $p = .949$, $\eta_p^2 = 1.326 \times 10^{-4}$.

Planned paired t-tests were conducted to assess differences between the first catch trial and the first baseline trial, as well as between the second catch trial and the second baseline trial. There were no significant differences between the first catch trials and their corresponding baseline trials, $t(31) = 0.729$, $p = .472$, Cohen's dz = 0.375, $BF_{01} = 4.143$, as well as the second catch trials and matched baseline trials, $t(31) = 0.797$, $p = .432$, Cohen's dz = 0.141, $BF_{01} = 3.951$.

1


(a)
Absolute Homing Error (°)
60
50
40
30
20
10
0
**
**
*
Familiarity
Standard
All Standard
Catch
All Baseline
Unmatched Baseline
Matched Baseline
Condition

2


(b)
Baseline
Catch
Absolute Homing Error (°)
60
50
40
30
20
10
0
24.811
24.107
19.865
19.646
1
2
Trial Number

3

Figure 6. (a) Absolute homing error for each condition in Experiment 3. Each dot represents one participant. (b) Absolute homing error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 2nd) in Experiment 3. The error bar was calculated by removing the error due to individual differences from the standard error of each trial.

Accepted in Journal of Experimental Psychology: Learning, Memory, and Cognition

4.3 Discussion

The results of Experiment 3 indicated that if participants believed the landmarks were hidden by the curtain, homing was not disrupted. Thus, the disruption in homing observed in Experiment 2 should be attributed to the mismatched views encountered after the outbound phase, rather than any disruption during the outbound phase. These findings favored updating-spatial-views hypothesis over the suppression hypothesis.

5. Experiment 4

In Experiment 4, we investigated whether diminishing landmark prevalence can mitigate this disruption. We already know that landmarks play a crucial role in navigation within familiar environments. Therefore, if we reduce the prevalence of landmarks, will that change the navigation methods of participants? Although the updating-spatial-views hypothesis did not give any prediction on it, it is possible that people update views of targets as well as landmarks to maintain orientations and locations as they move through the environment. When we increase the importance of target objects and decrease the prevalence of landmarks, updating spatial views of targets might be more important than updating spatial views of landmarks. As a result, removal of landmarks (i.e., mismatch view of landmarks) on the catch trial may not disrupt orientation.

Given that cognitive resources are limited, individuals tend to allocate these resources wisely, focusing on updating spatial views of the most relevant and reliable cues during navigation. In Experiment 4, we increased the number of targets from three to five, exceeding the number of landmarks (i.e., three towers). This shift in the target-to-landmark ratio was intended to encourage participants to engage in spatial updating based on the targets rather than the landmarks. Additionally, the targets were arranged in a square with the home target at the center (see Figure 7). Compared to a single target or the triangular arrangement used in previous experiments, a square introduces a more regular and stable geometric shape, which is easier to remember and update. This organized spatial layout of targets further encourages participants to rely on the targets for spatial updating rather than the landmarks.

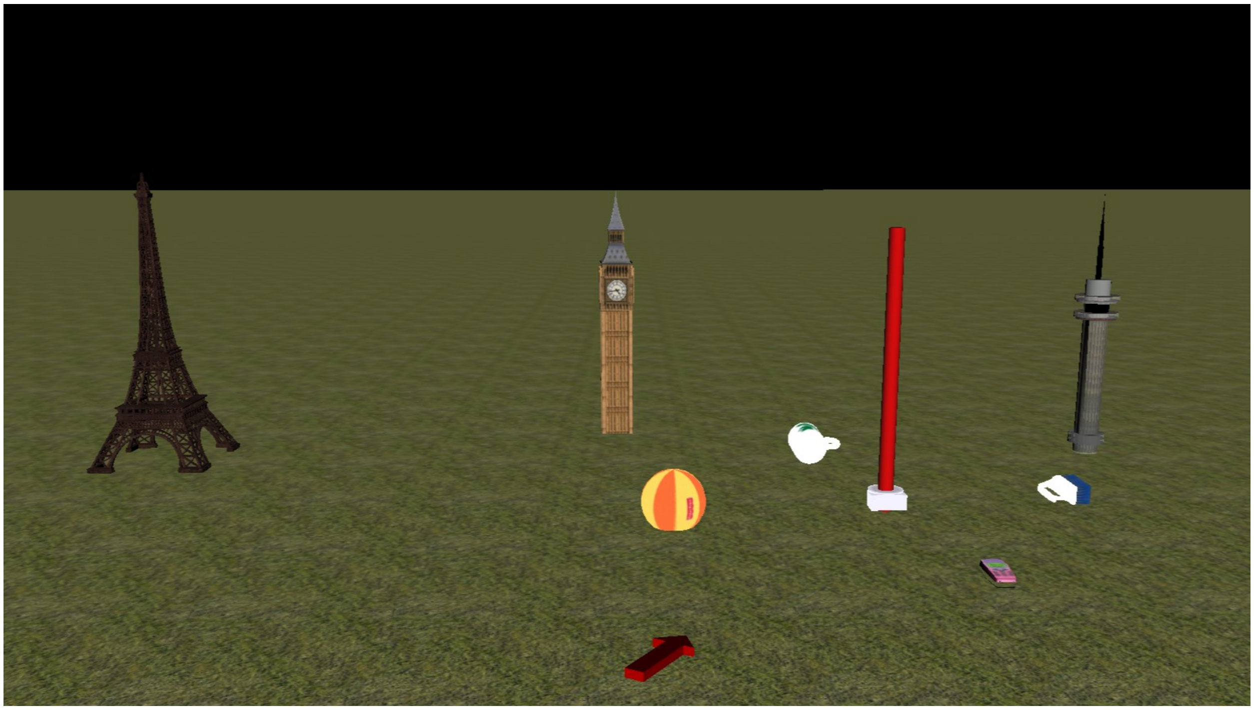


Figure 7. A screenshot of a sample trial in the virtual environment featuring three visual landmarks: the first red pole (the home object's location, O), the possible location of the object array in Experiments 4 and 5, and the start location (S), which is indicated by using a red arrow to show the initial facing direction.

5.1 Method

5.1.1 Participants

Thirty-two university students (16 females, 16 males) with normal or corrected-to-normal vision and be able to walk independently participated as partial fulfillment of a requirement for their introductory psychology courses.

5.1.2 Materials, design, and procedures

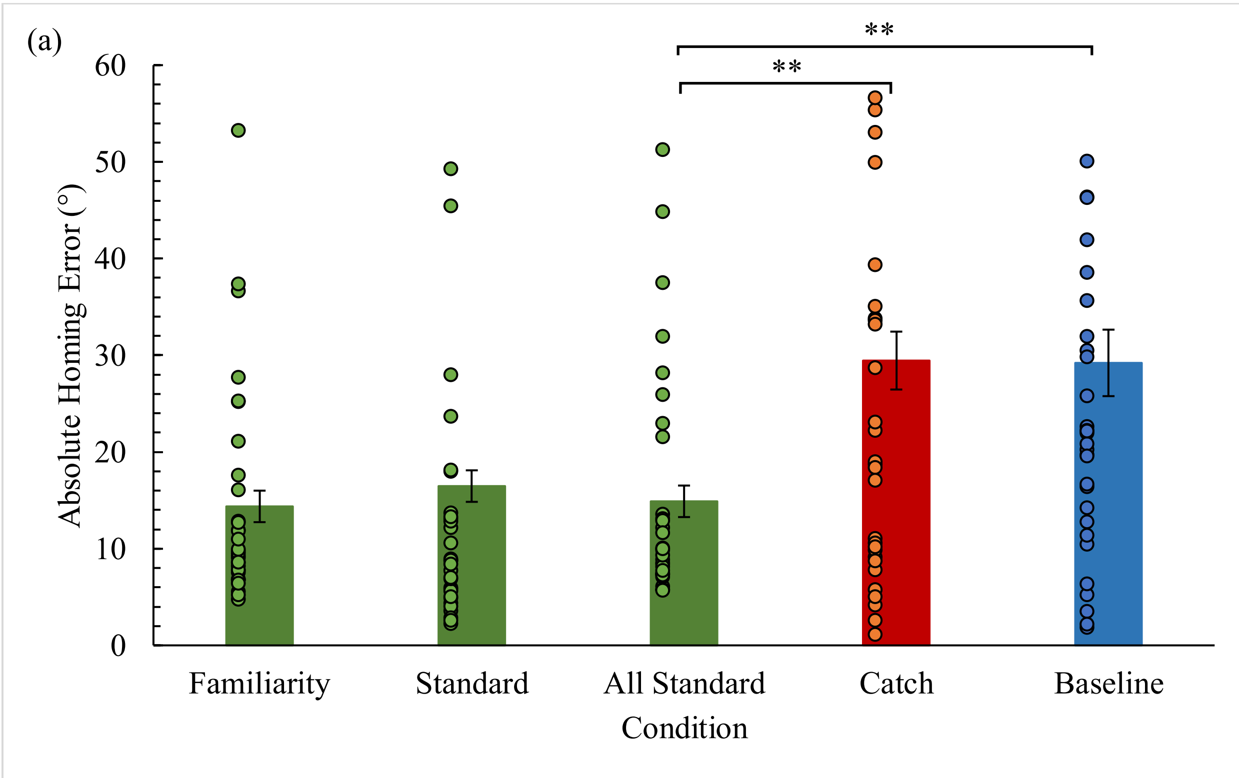
Experiment 4 was conducted in a manner similar to Experiment 1, with the following modifications: we utilized five objects as targets, specifically a clock, a ball, a brush, a mug, and a phone. The two additional objects were positioned 1.41 meters from the home, respecting the participants' initial facing direction (red arrow, S), in the direction of 135° clockwise or counter-clockwise (see Figure 7). Same as Experiment 1, across participants, three objects randomly appeared at the three locations whereas within each participant, the association between objects and locations was fixed across trials. Furthermore, we eliminated the two unmatched baseline trials that preceded the matched baseline trials, resulting in a total of 16 trials. Similar to Experiment 1, participants were asked to first retrieve the location of the center object and then the locations of the other four objects in a random order during the homing phase of the catch and baseline trials. Additionally, following Experiments 2 and 3, we used a black curtain to hide and reveal the landmarks between the outbound phase and homing phase.

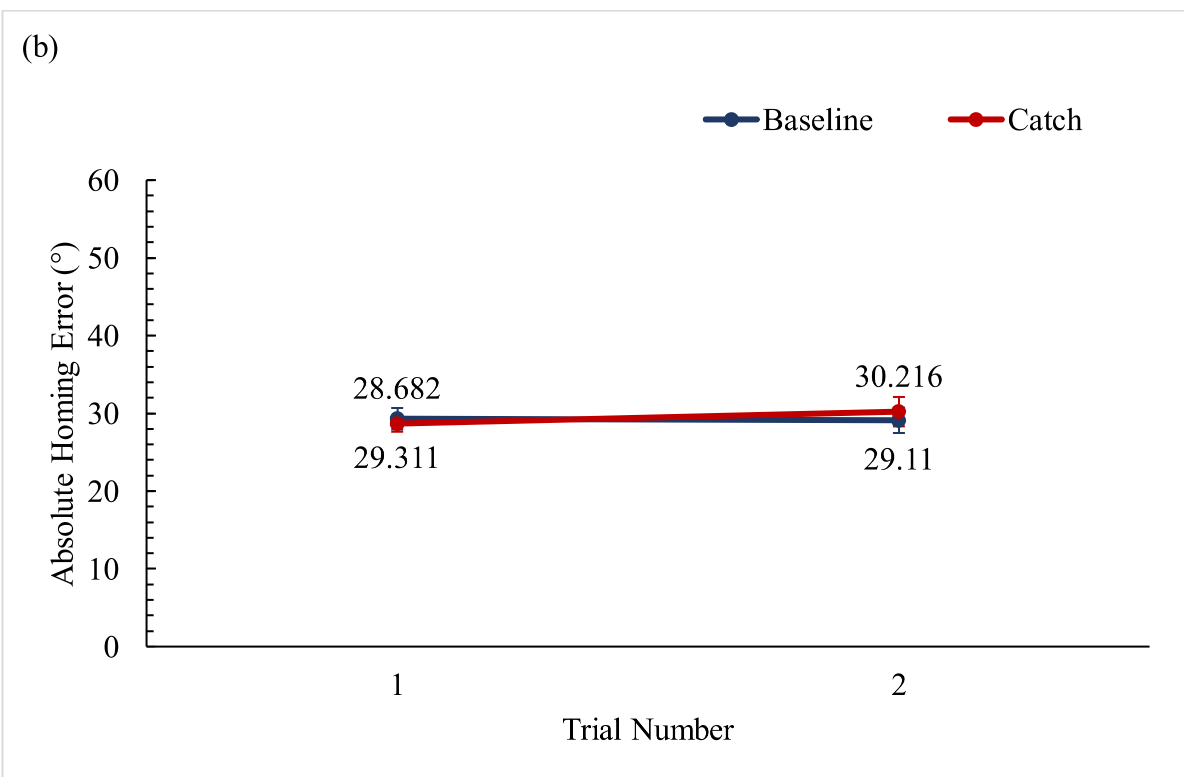
5.2 Results

The figure 8a shows the overall mean absolute homing error for each condition. There was no significant difference in the mean absolute homing error between the familiarity trials and standard trials, $t(31) = -0.671$, $p = .507$, Cohen's $dz = -0.119$, $BF_{01} = 4.300$. Consequently, we compared the mean absolute error among the all 12 standard trials (9 familiarity trials and 3 standard trials), the catch trials, and the baseline trials. The main effect remained significant after the Huynh-Feldt correction ($\varepsilon = 1$), $F(2, 66.145) = 6.958$, $p = .002$, $MSE = 2222.851$, $\eta_p^2 = .183$. Post-hoc testing using Bonferroni correction revealed the following significant differences: the homing error was significantly smaller in the standard trial condition than in the catch trial condition (mean difference = -14.554, $p = .005$, Cohen's *dz* = -0.650) and baseline trial condition (mean difference = -14.315, $p = .006$, Cohen's *dz* = -0.639). In addition, the homing error in the catch trial condition was comparable in the baseline trials condition (mean difference = 0.239, $p = 1.000$, Cohen's *dz* = 0.011).

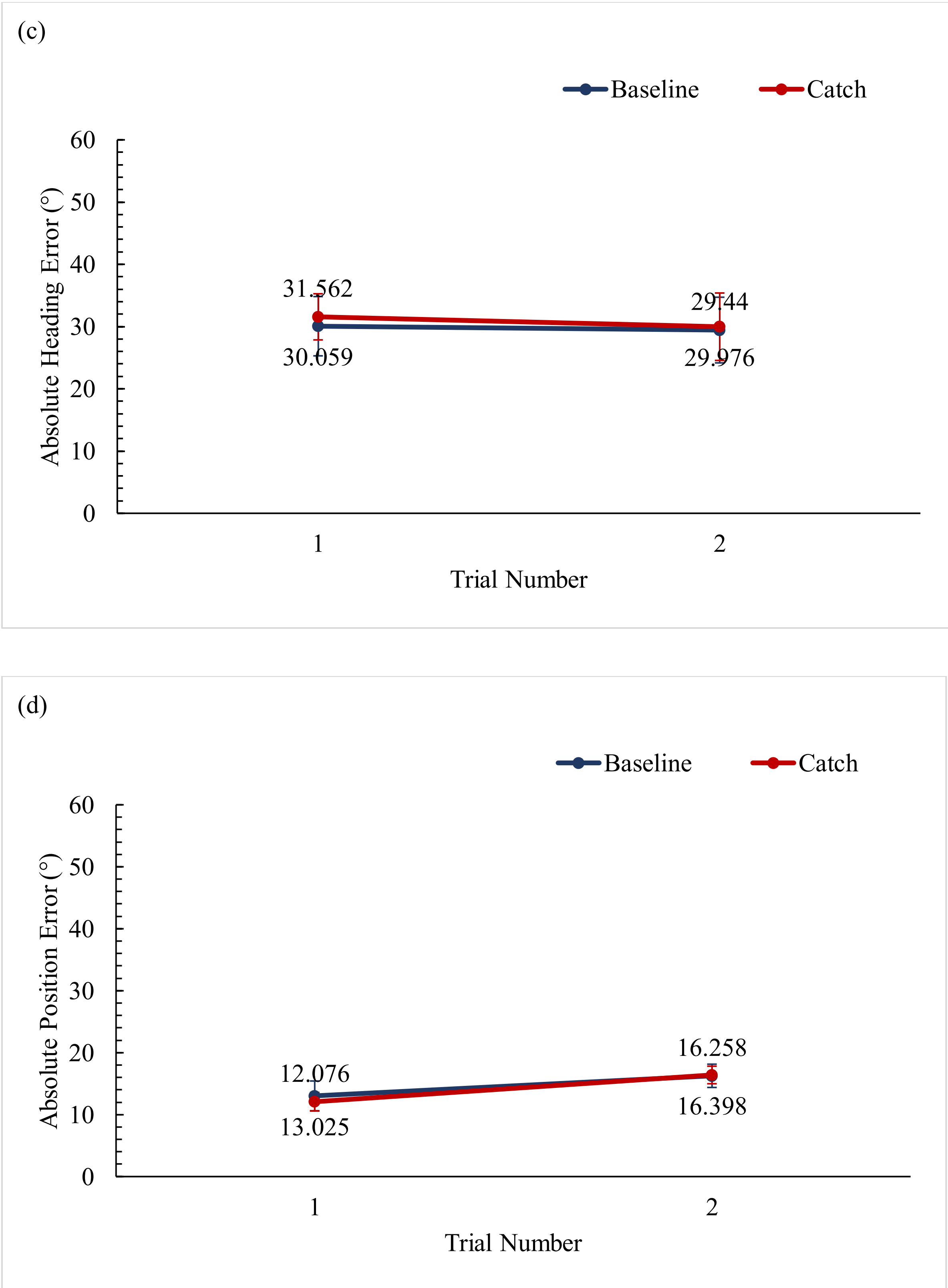
Figures 8b, 8c, and 8d illustrate the absolute homing error, absolute heading error, and absolute position error, respectively, for each catch trial and its matched baseline trials. Across all paired trials, the analyses reveal that there are no statistically significant differences between the errors. Specifically, for homing errors, a repeated measures ANOVA was conducted to examine the effect of the trial type (catch vs. baseline) and trial sequence (the first trial vs. the second trial) on homing error. There was no significant main effect of trial type, $F(1, 31) = 0.003$, $p = .959$, $\eta_p^2 = 8.838\text{x}10^{-5}$, nor was there a significant main effect of trial sequence, $F(1, 31) = 0.019$, $p = .892$, $\eta_p^2 = 6.012\text{x}10^{-4}$. The interaction between trial type and trial sequence was also not significant, $F(1, 31) = 0.030$, $p = .863$, $\eta_p^2 = 9.822\text{x}10^{-4}$.

Planned paired t-test were performed to access the differences between the first catch trial and first baseline trial, as well as between the second catch trial and second baseline trial. The comparison between the first catch trial and its matched baseline trial yielded $t(31) = -0.091$, $p = .982$, Cohen's *dz* = -0.016, $BF_{01} = 5.275$, indicating substantial evidence for the null hypothesis. The second catch trial and its corresponding baseline trial showed $t(31) = 0.168$, $p = .868$, Cohen's *dz* = 0.030, $BF_{01} = 5.226$. For heading errors, the first catch and its matched baseline trial had $t(31) = 0.230$, $p = .820$, Cohen's $dz = 0.041$, $BF_{01} = 5.167$. The second catch and its corresponding baseline trial resulted in $t(31) = 0.076$, $p = .940$, Cohen's $dz = 0.013$, $BF_{01} = 5.281$. Lastly, for position errors, the first catch and its matched baseline trial recorded $t(31) = -0.391$, $p = .699$, Cohen's $dz = -0.069$, $BF_{01} = 4.933$. The second catch and its corresponding baseline trial had $t(31) = 0.058$, $p = .954$, Cohen's $dz = 0.010$, $BF_{01} = 5.287$. These results indicate a lack of significant differences in all three types of errors across the paired trials.


(a)
**
**
60
50
40
30
20
10
0
Absolute Homing Error (°)
Familiarity
Standard
All Standard
Catch
Baseline
Condition


(b)
Baseline
Catch
60
50
40
30
20
10
0
Absolute Homing Error (°)
28.682
29.311
30.216
29.11
1
2
Trial Number

Accepted in Journal of Experimental Psychology: Learning, Memory, and Cognition



Accepted in Journal of Experimental Psychology: Learning, Memory, and Cognition

Figure 8. (a) Absolute homing error for each condition in Experiment 4. Each dot represents one participant. (b) Absolute homing error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 2nd) in Experiment 4. The error bar was calculated by removing the error due to individual differences from the standard error of each trial. (c) Absolute heading error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 2nd) in Experiment 4. The error bar was calculated by removing the error due to individual differences from the standard error of each trial. (d) Absolute position error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 2nd) in Experiment 4. The error bar was calculated by removing the error due to individual differences from the standard error of each trial.

5.3 Discussion

As the number of objects increased and the objects formed a regular layout to decrease the prevalence of landmarks, the impairment of homing error and heading error in the first catch trial disappeared, suggesting that reducing the prevalence of landmarks could mitigate orientation disruption. All the visual features in the environment could be used to help participant keep oriented. As the prevalence of landmarks decreased, participants might have placed more emphasis on the spatial views of the layout of objects, thereby minimizing the disruption caused by the removal of stable landmarks. However, does this mean when prioritizing spatial views of objects over landmarks, navigators completely disregard the stable landmarks? Experiment 5 tackled this question.

6. Experiment 5

In Experiment 5, we investigated whether participants completely ignore landmarks in an environment with a low prevalence of landmarks. Similar to previous experiments, the first catch trial was designed to create an unexpected situation. However, in the second catch trial of Experiment 5, instead of removing the landmarks, we rotated them. This provided participants with familiar landmarks, but in a location which the landmarks rotated as a group 100° clockwise or counter-clockwise.

6.1 Method

6.1.1 Participants

Thirty-two university students (16 females, 16 males) with normal or corrected-to-normal vision and be able to walk independently participated as partial fulfillment of a requirement for their introductory psychology courses.

6.1.2 Materials, design, and procedures

Experiment 5 was identical to Experiment 4, with the following modifications: The most significant difference was in the second catch trials, where landmarks were rotated as a group by 100°, either clockwise or counter-clockwise, randomized across trials. Similar to Experiments 2 and 3, there were a total of 18 trials: the first nine were standard trials (also termed familiarity trials in the results section), followed by the first catch trial, three additional standard trials, and then the second catch trial. The final four trials were baseline trials, with the first two classified as unmatched baseline trials and the latter two as matched baseline trials. Participants were not informed that the landmarks were rotated in the homing phase of the second catch trials.

6.2 Results

Figure 9a displays the overall mean absolute homing error for each condition. There was a significant difference in the mean absolute homing error between the familiarity trials and standard trials, $t(31) = 2.300$, $p = .028$, Cohen's $dz = 0.407$, $BF_{01} = 0.542$. However, the mean absolute homing error did not significantly differ between the unmatched baseline trials and the matched baseline trials, $t(31) = 0.175$, $p = .862$, Cohen's $dz = 0.031$, $BF_{01} = 5.220$. Consequently, we compared the mean absolute error among the three standard trials (the ones between two catch trials), the catch trials, and all 4 baseline trials (2 unmatched baseline trials and 2 matched baseline trials). The main effect remained significant after the Huynh-Feldt correction ($\varepsilon = 0.940$), $F(1.881, 58.298) = 82.319$, $p < .001$, $MSE = 30662.227$, $\eta_p^2 = .727$. Post-hoc testing using Bonferroni correction revealed the following significant differences: the homing error was significantly smaller in the standard trial condition than in the catch trial condition (mean difference = -58.272, $p < .001$, Cohen's $dz = -2.954$) and baseline trial condition (mean difference = -16.639, $p = .002$, Cohen's $dz = -0.844$). In addition, the homing error in the catch trial condition was significantly larger than in the baseline trials condition (mean difference = 41.634, $p < .001$, Cohen's *dz* = 2.111).

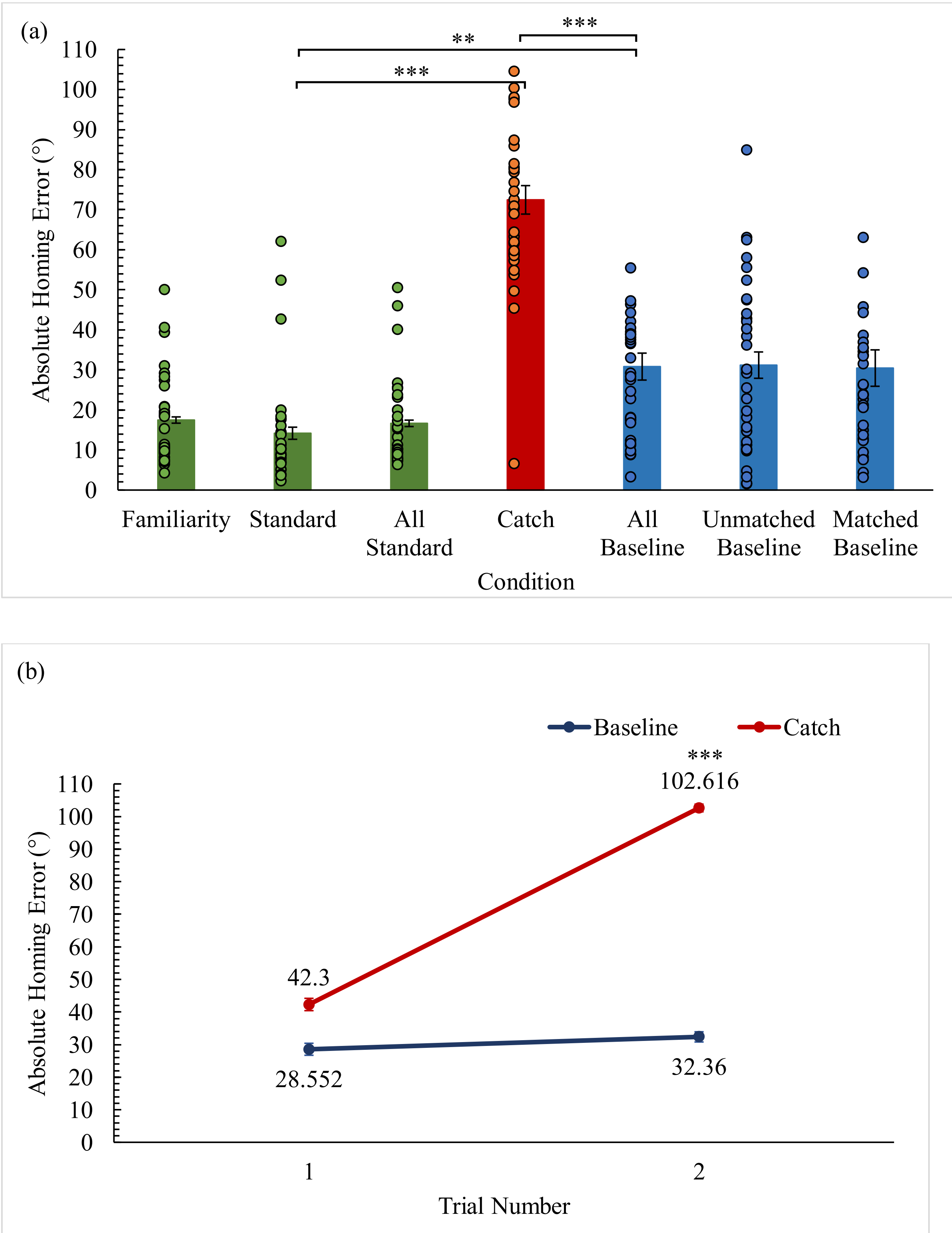
Figure 9b depicts the absolute homing error for each catch trial and its matched baseline trials. A repeated measures ANOVA was conducted to examine the effect of the trial type (catch vs. baseline) and trial sequence (the first trial vs. the second trial) on homing error. The main effect of trial type was significant, $F(1, 31) = 43.624$, $p < .001$, $\eta_p^2 = .585$, indicating that the homing error in the catch trial condition was significant different from baseline trial condition. The main effect of type sequence was also significant, $F(1, 31) = 74.477$, $p < .001$, $\eta_p^2 = .706$. The interaction between trial type and trial sequence was also significant, $F(1, 31) = 29.830$, $p < .001$, $\eta_p^2 = .490$.

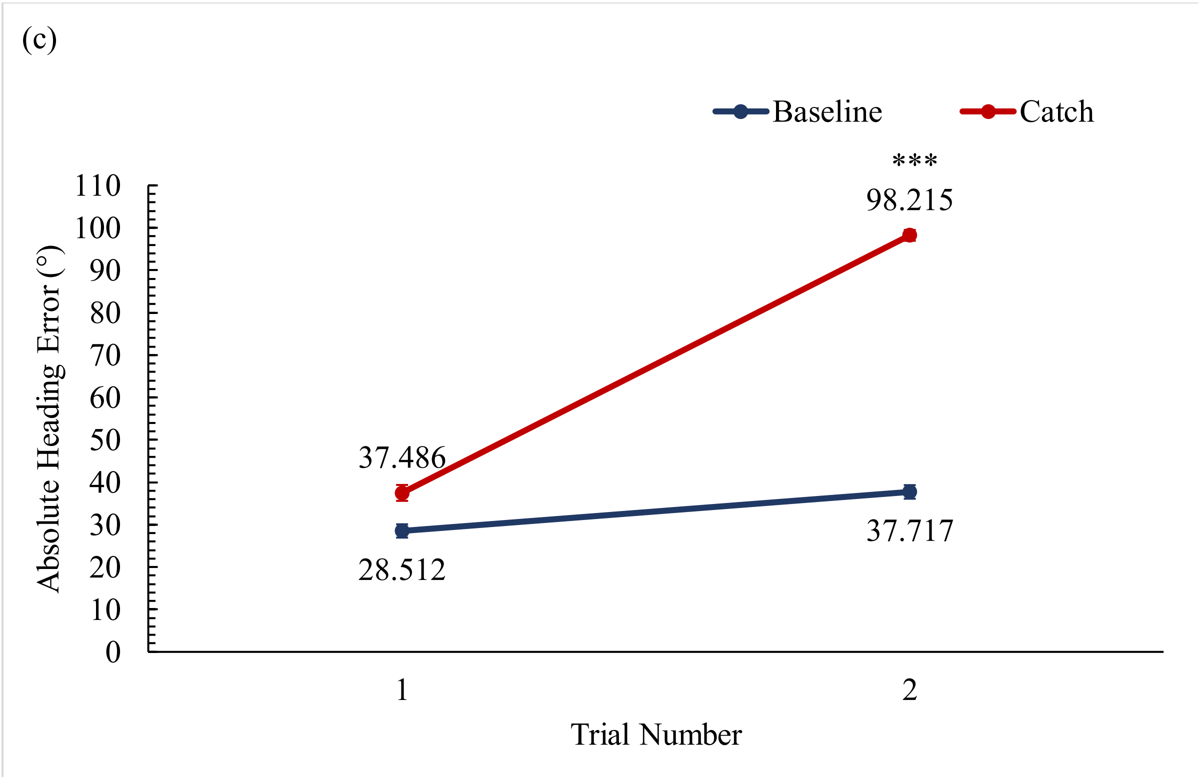
Planned paired t-tests were performed to access the differences between the first catch trial and first baseline trial, as well as between the second catch trial and second baseline trial. The homing error in the first catch trial is statistically the same with the first matched baseline trial, $t(31) = 1.447$, $p = .158$, Cohen's *dz* = 0.256, $BF_{01} = 2.059$. However, the homing error in the second catch trial is significantly larger than its matched baseline trial, $t(31) = 10.577$, $p < .001$, Cohen's *dz* = 1.870, $BF_{01} = 9.281\text{x}10^{-13}$.

Figure 9c shows the absolute heading error for each catch trial and its matched baseline trials. Similar to the pattern in the absolute homing error, the heading error in the first catch trial is comparable to the corresponding baseline trial, $t(31) = 1.006$, $p = .322$, Cohen's *dz* = 0.178, $BF_{01} = 3.328$. However, the heading error in the second catch trial is significantly larger than its matched baseline trial, $t(31) = 8.836$, $p < .001$, Cohen's *dz* = 1.562, $BF_{01} = 5.123\text{x}10^{-11}$.

Accepted in Journal of Experimental Psychology: Learning, Memory, and Cognition

Figure 9d demonstrates the absolute position error for each catch trial and its matched baseline trials. The heading error in the first catch trial is comparable to its matched baseline trial, $t(31) = -1.776$, $p = .086$, Cohen's $dz = -0.314$, $BF_{01} = 1.304$. Similar, the position error in the second catch trial is comparable to the second matched baseline trial, $t(31) = -1.530$, $p = .136$, Cohen's $dz = -0.270$, $BF_{01} = 1.849$.


(a)
Absolute Homing Error (°)
110
100
90
80
70
60
50
40
30
20
10
0
***
**
***
Familiarity
Standard
All Standard
Catch
All Baseline
Unmatched Baseline
Matched Baseline
Condition
(b)
Baseline
Catch
***
102.616
42.3
28.552
32.36
Absolute Homing Error (°)
110
100
90
80
70
60
50
40
30
20
10
0
1
2
Trial Number


(c)
Baseline
Catch
***
98.215
37.486
37.717
28.512
Absolute Heading Error (°)
110
100
90
80
70
60
50
40
30
20
10
0
1
2
Trial Number

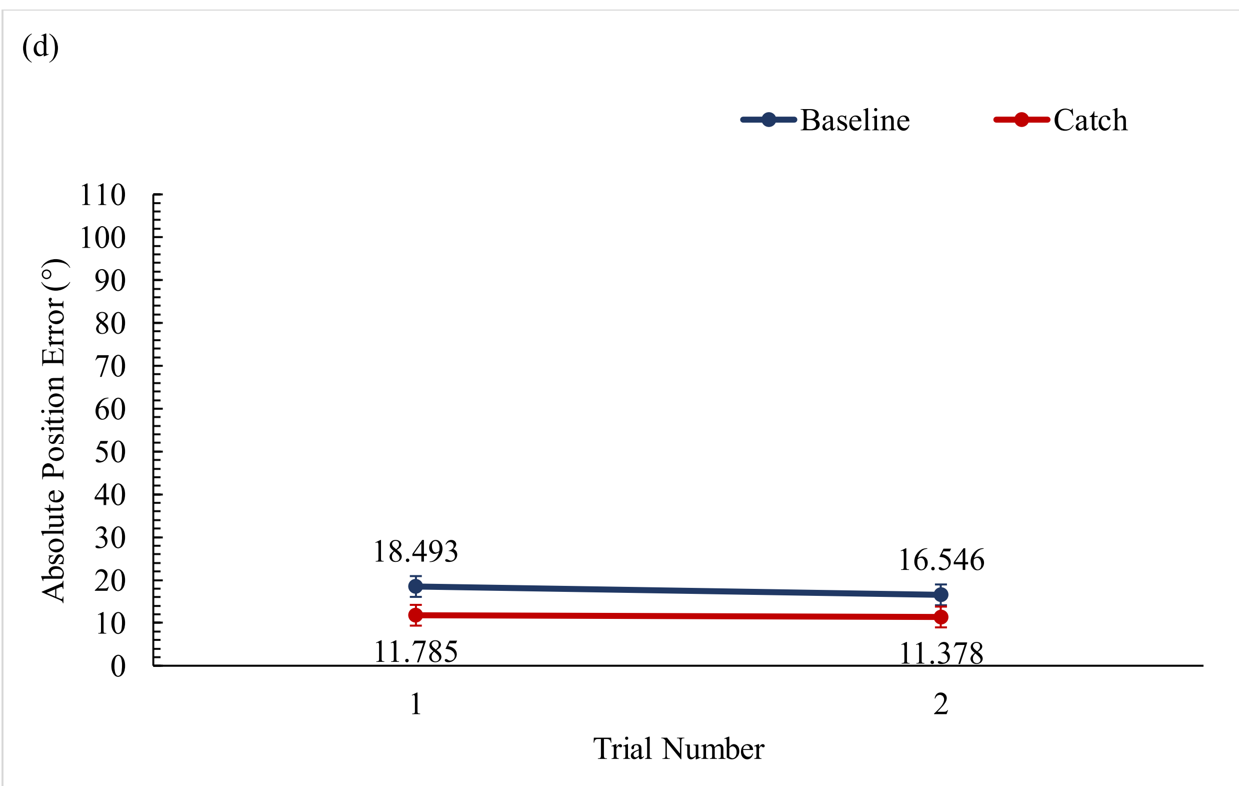

(d)
Baseline
Catch
18.493
16.546
11.785
11.378
Absolute Position Error (°)
110
100
90
80
70
60
50
40
30
20
10
0
1
2
Trial Number

Figure 9. (a) Absolute homing error for each condition in Experiment 5. Each dot represents one participant. (b) Absolute homing error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 2nd) in Experiment 5. The error bar was calculated by removing the error due to individual differences from the standard error of each trial. (c) Absolute heading error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 2nd) in Experiment 5. The error bar was calculated by removing the error due to individual differences from the standard error of each trial. (d) Absolute position error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 2nd) in Experiment 5. The error bar was calculated by removing the error due to individual differences from the standard error of each trial.

6.3 Discussion

The results of the first catch trial replicated what we found in Experiment 4, showing no homing or heading disruption when there were five objects. Furthermore, we observed that both the homing and heading errors in the second catch trial were approximately 100° (i.e., 102.616° for the homing error in the second catch trial and 98.215° for the heading error in the second catch trial), closely matching the rotation angle (i.e., 100°). This demonstrates that participants indeed utilized the rotated familiar landmarks for orientation. Therefore, while reducing the prevalence of landmarks lessens the disruption, participants still relied on the landmarks, especially for orientation, when they were available. In contrast, the position errors in the second catch trial did not increase with the homing and heading errors, which increased together. The results indicated that the pattern of the absolute homing error was similar to that of the absolute heading error, but distinct from the absolute position error, confirming the conclusion of Experiment 1 that the disrupted homing was attributed to the disrupted heading estimates rather than position estimates.

8. General Discussion

This study aimed to uncover the cognitive mechanisms behind the disruptive effect of removing anticipated landmarks on individuals' homing performance, thereby understanding the role of path integration in a familiar environment with constantly available landmarks. In particular, it investigated when this disruption occurs, which spatial representations are impacted, and whether lessening landmark prevalence mitigates this disruption. It yielded three important findings. First, the removal of anticipated landmarks disrupted participants' heading and homing estimates, but not their position estimates. Second, this disruption in homing occurred when participants noticed the removal of landmarks after the curtain was raised, but not when the curtain remained unraised to obscure their views of the environment. Third, reducing the prevalence of landmarks mitigated the disruption in heading/homing; however, participants still relied on the available familiar landmarks for orientation/homing. These findings significantly advance our understanding of the interaction between path integration and piloting in navigation within a familiar environment.

The first two findings distinguish the two hypotheses conceptualizing different roles of path integration in a familiar environment (Chen and Mou, 2024). The suppression hypothesis posits that, in a familiar environment, path integration is redundant and wasteful because piloting dominates (Zhao & Warren, 2015a). In contrast, the updating-spatial-views hypothesis posits that path integration in a familiar environment is used to update spatial views of the environment to make place/scene recognition more effective, facilitating piloting. Chen and Mou (2024) demonstrated that spatial representations created from path integration were used to resolve the spatial ambiguity of two targets or two groups of landmarks. Nevertheless, Chen and Mou (2024) did not provide direct evidence to eliminate the possibility that spatial representations for homing, which might differ from those for recognition, might still be impaired due to suppression in path integration. However, using the homing paradigm rather than the recognition paradigm, the current study provided strong evidence to refute this possibility.

The suppression hypothesis fails to account for the dissociation between disrupted heading estimates and intact position estimates observed in the first catch trial of Experiment 1 in the current study. According to the suppression hypothesis, path integration is suppressed during walking along the outbound path. If path integration were indeed suppressed during walking, it would impair the updating of both heading and position representations. Consequently, both heading and position estimates should be impaired during the homing phase. Moreover, the suppression hypothesis cannot explain the finding that the appearance/disappearance of homing disruption was modulated by the raised/unraised curtain in Experiments 2 and 3. If spatial representations were impaired during walking prior to the curtain manipulation in the homing phase, as suggested by the suppression hypothesis, then impaired spatial representations should lead to impaired homing performance regardless of the curtain manipulation. Hence, the suppression hypothesis predicts homing disruption in Experiment 3 as well. Therefore, these findings, which were based on homing rather than recognition responses, still undermine the suppression hypothesis.

In contrast, the updating-spatial-views hypothesis accounts for the observed dissociation between disrupted heading estimates and intact position estimates in Experiment 1. According to this hypothesis, spatial representations are disrupted after the outbound phase and during the homing phase. Previous studies have showed that although heading estimates and position estimates are dependent during walking (Zhang et al., 2020), they are independent after walking and can be selectively impaired (Mou & Zhang, 2014; Zhang & Mou, 2017, 2019). Therefore, the dissociation between disrupted heading estimates and intact position estimates is not inconsistent with the updating-spatial-views hypothesis. The updating-spatial-views hypothesis can also explain why the appearance/disappearance of homing disruption was modulated by the raised/unraised curtain in Experiments 2 and 3. The updating-spatial-views hypothesis proposes that mismatched views cause disorientation. While the raised curtain revealed mismatched views, causing homing disruption, the unraised curtain concealed views, preventing mismatched views (Rolls, 1999, 2023), and thus not causing homing disruption.

Therefore, the current findings favor the updating-spatial-views hypothesis over the suppression hypothesis, using the homing paradigm. In addition, the finding that mismatched spatial views disrupted participants' heading estimates but not position estimates significantly enriches the updating-spatial-views hypothesis. Although the original updating-spatial-views hypothesis can account for dissociation between heading and position estimations after walking, it did not clearly specify whether disorientation affected heading estimates, position estimates, or both. The revised version of the updating-spatial-views hypothesis then specifies that mismatched spatial views disrupt individuals' heading estimates, which leads to disrupted homing estimates.

The findings from Experiments 4 and 5, which showed that reducing the prevalence of landmarks mitigated disruptions in heading/homing, suggest that individuals are capable of prioritizing spatial views of items in the environment. This extends the updating-spatial-views hypothesis further. In Experiments 4 and 5, the use of five objects forming a regular layout led to the disappearance of disrupted homing/heading, which was caused by the unexpected removal of anticipated landmarks. This suggests that participants may have prioritized the object array over landmarks, thereby mitigating the disruption caused by the removal of anticipated landmarks.

Notably, despite a decreased prevalence of landmarks in Experiment 5, participants continued to orient themselves according to the rotated landmarks. The rotated landmarks caused the rotated orientation, which then led to the rotated homing estimates. This finding indicates that participants did not completely disregard landmarks, even when prioritizing spatial views of the object layout. This aligned with Chen and Mou (2024), which showed that participants updated spatial views of targets since they could recognize the correct target from the rotated one even when spatial views of landmarks were prioritized. Therefore, participants might update several spatial views of environments while prioritizing one of them. Furthermore, even with their reduced prevalence, landmarks continued to dominate over path integration in determining orientations, underscoring the prevailing role of landmarks, compared to path integration, in determining locations and orientations (Etienne & Jeffery, 2004; Etienne et al., 1998; Mou & Zhang, 2014; Zhang et al., 2020; Zhao & Warren, 2015b).

An additional significant theoretical contribution of this study is the theoretical proposal that mismatched spatial views more easily disrupt heading representations than position representations updated by path integration. Previous studies have theorized that people can selectively impair heading or position representations by using a rotated distal landmark (Mou & Zhang, 2014) or by displacing proximal landmarks to the testing positions (Zhang & Mou, 2017). The current study conjectures for the first time that, after walking, heading estimates are more susceptible to disruption than position estimates, for three reasons. 1. Research in human spatial cognition often utilizes a disorientation method that spins participants in place (e.g., Wang & Spelke, 2000), disrupting their orientation without affecting their position representation (Zhang et al., 2020). Currently, there is no disorientation method capable of disrupting participants' position without also disrupting their orientation representations. 2. Maintaining position representations is more crucial than maintaining heading representations because individuals need to recognize their current location to activate the relevant knowledge for interacting with that specific place. For instance, the necessity to work is determined by being in an office, not by facing a particular direction. 3. Individuals can change their orientation more rapidly than their position at natural speed. This bodily constraint might also contribute to the more reliable maintenance of position representations over heading representations (Khobkhun et al., 2021).

Providing initial evidence to support the theoretical conjecture that it is easier to disrupt heading than position representations after walking, Experiment 1 of this study demonstrated that

Accepted in Journal of Experimental Psychology: Learning, Memory, and Cognition

an empty ground without landmarks in the first catch trial disrupts participants' heading estimates but not their position estimates. However, future studies should explore this conjecture more broadly. For instance, numerous studies have shown that developing a global heading representation while standing in an indoor environment is challenging for people (Lei & Mou, 2023; Marchette et al., 2014; Wang & Brockmole, 2003). It would be important to test whether individuals, while standing in a room, can maintain their position representations relative to the global environment outside the room although they cannot maintain their global heading representations.

Compared with Experiment 2, Experiment 3 demonstrated that participants' homing estimates were not disrupted when the curtain unexpectedly remained unraised during the first catch trial. This indicates that surprise or unexpectedness, in itself, does not necessarily lead to disorientation. Instead, it appears that disorientation resulted from the unexpected absence of landmarks. This finding is consistent with the findings that unexpectedly presenting two groups of landmarks/targets did not disorient participants observed in Chen and Mou (2024). However, we do not exactly know the relationship by general surprise and navigation. Previous studies have showed that surprise events could draw attention away from the current task (Horstmann, 2015). In addition, surprise events might impair hippocampal functions, which is important for navigation (Sinclair et al., 2021; Wolbers & Hegarty, 2010). Future studies should investigate whether other forms of unexpectedness can also lead to disorientation.

We acknowledge that while Experiments 4 and 5 demonstrated that reducing the importance of landmarks could mitigate disruptions in homing caused by their sudden removal, the specific factors that influence the prioritization of items in updating spatial views during path integration remain unclear. The observed homing disruptions due to mismatched views of landmarks occurred with one and three objects in Experiments 1 and 2 but disappeared with five objects in Experiments 4 and 5. We should be cautious before concluding that five objects represent a threshold number necessary to eliminate homing disruptions.

Indeed, the object number may not be the sole influencing factor. In Experiments 4 and 5, the regular shape formed by the five objects might also play a crucial role in reducing the importance of landmarks. Such a regular layout might enable participants to establish an intrinsic reference system based on the layout of object (Mou & McNamara, 2002), allowing them to update their orientation and position relative to this reference system (Zhang et al., 2011). Additionally, the locations of the landmarks could also be encoded relative to the intrinsic reference system defined by the layout of objects. Therefore, while the rotated landmarks might facilitate recovering the intrinsic reference directions, leading to rotated orientations observed in the second catch trial of Experiment 5, the removal of landmarks could not indicate reference systems, leading to diminished homing disruption in the first catch trial of Experiments 4 and 5. Future studies are needed to examine exact important factors that affect prioritizing items in updating spatial views.

Notably, the updating-spatial-views hypothesis posits that updating spatial views in a familiar environment could facilitate piloting (i.e., place/scene recognition). However, it is not clear whether in a familiar environment, the rich visual feedback of the outcome of path integration could also facilitate path integration (Philbeck & O'Leary, 2005; Rieser, 1999). Since the pioneer experiment of Zhao and Warren (2015a), the baseline trials have always been placed in the last few trials. It is important to investigate whether homing performance in these trials might have been enhanced by the repeated standard trials preceding them as well. The always encountering landmarks in those earlier trials might calibrate and facilitate path integration. Even in the later trials without landmarks, this facilitation due to calibration still lasts (Tcheang et al., 2011; Du et al., 2020). If it is true, when baseline trials are moved prior to the standard trials, participants' performance in homing would significantly become worse. Future studies should test whether visual landmarks facilitate path integration as well.

In conclusion, this study helps us understand more about how we find our way around by looking at how important landmarks are and when their absence affects our ability to orient ourselves. By adding to the updating-spatial-views hypothesis, our findings showed that spatial views of environments including objects and landmarks are updated by path integration. The absence of anticipated primary spatial views disrupts people's orientation representations. Although reducing the prevalence of landmarks reduces this disruption, landmarks are not ignored and still used to indicate orientation.

References

Amorim, M., Glasauer, S., Corpinot, K, & Berthoz, A. (1997). Updating an object's orientation and location during nonvisual navigation: A comparison between two processing modes. *Perception & Psychophysics, 59*(3), 404-418. https://doi.org/10.3758/BF03211907

Chen, Y., & Mou, W. (2024). Path integration, rather than being suppressed, is used to update spatial views in familiar environments with constantly available landmarks. *Cognition, 242*, 105662-105662. https://doi.org/10.1016/j.cognition.2023.105662

Du, Y., Mou, W., & Zhang, L. (2020). Unidirectional influence of vision on locomotion in multimodal spatial representations acquired from navigation. *Psychological Research, 84*(5), 1284-1303. https://doi.org/10.1007/s00426-018-1131-3

Etienne, A. S., & Jeffery, K. J. (2004). Path integration in mammals. *Hippocampus, 14*(2), 180-192. https://doi.org/10.1002/hipo.10173

Etienne, A. S., Maurer, R., Berlie, J., Reverdin, B., Rowe, T., Georgakopoulos, J., & Séguinot, V. (1998). Navigation through vector addition. *Nature, 396*(6707), 161-164. https://doi.org/10.1038/24151

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*(2), 195-215. https://doi.org/10.1037/0278-7393.31.2.195

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

Gallistel, C. R., & Matzel, L. D. (2013). The neuroscience of learning: Beyond the Hebbian synapse. *Annual Review of Psychology, 64*(1), 169-200. https://doi.org/10.1146/annurev-psych-113011-143807

Hermer, L., & Spelke, E. (1996). Modularity and development: The case of spatial reorientation. *Cognition, 61*(3), 195-232. https://doi.org/10.1016/S0010-0277(96)00714-7

Horstmann, G. (2015). The surprise-attention link: A review. *Annals of the New York Academy of Sciences, 1339*(1), 106–115. https://doi.org/10.1111/nyas.12679

Khobkhun, F., Hollands, M., & Richards, J. (2021). The effect of different turn speeds on whole-body coordination in younger and older healthy adults. *Sensors (Basel, Switzerland), 21*(8), 2827. https://doi.org/10.3390/s21082827

Lei, X., & Mou, W. (2023). Visual re-anchoring in misaligned local spaces impairs global path integration. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 49*(5), 728-742. https://doi.org/10.1037/xlm0001229

Loomis, J. M., Klatzky, R. L., Golledge, R. G., & Philbeck, J. W. (1999). Human navigation by path integration. In R. G. Golledge (Ed.), *Wayfinding behavior: Cognitive mapping and other spatial processes* (pp. 125-151). Washington, DC: American Psychological Association.

Marchette, S. A., Vass, L. K., Ryan, J., & Epstein, R. A. (2014). Anchoring the neural compass: Coding of local spatial reference frames in human medial parietal lobe. *Nature Neuroscience, 17*(11), 1598-1606. https://doi.org/10.1038/nn.3834

Mou, W., & McNamara, T. P. (2002). Intrinsic frames of reference in spatial memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 28*, 162-170.

Mou, W., & Qi, Y. (2024). Human spatial navigation: benchmark behavioral findings. In S. Della Sala (Ed.), *Encyclopedia of the Human Brain (2nd ed.)*. Elsevier.

Mou, W., & Wang, L. (2015). Piloting and path integration within and across boundaries. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 41*(1), 220-234. https://doi.org/10.1037/xlm0000032

Mou, W., & Zhang, L. (2014). Dissociating position and heading estimations: Rotated visual orientation cues perceived after walking reset headings but not positions. *Cognition, 133*(3), 553-571. https://doi.org/10.1016/j.cognition.2014.08.010

Nardini, M., Jones, P., Bedford, R., & Braddick, O. (2008). Development of cue integration in human navigation. *Current Biology, 18*(9), 689-693. https://doi.org/10.1016/j.cub.2008.04.021

Newman, P. M., Qi, Y., Mou, W., & McNamara, T. P. (2023). Statistically optimal cue integration during human spatial navigation. *Psychonomic Bulletin & Review, 30*(5), 1621-1642. https://doi.org/10.3758/s13423-023-02254-w

Philbeck, J. W., & O'Leary, S. (2005). Remembered landmarks enhance the precision of path integration. *Psicológica (Valencia), 26*(1), 7–24.

Philbeck, J. W., Klatzky, R. L., Behrmann, M., Loomis, J. M., & Goodridge, J. (2001). Active control of locomotion facilitates nonvisual navigation. *Journal of Experimental Psychology: Human Perception and Performance, 27*(1), 141.

Rieser, J. J. (1999). Dynamic spatial orientation and the coupling of representation and action. In R. G. Golledge (Ed.), *Wayfinding Behavior: Cognitive Mapping and Other Spatial Processes (pp. 168–190).* Baltimore: JHU Press.

Rolls, E. T. (1999). Spatial view cells and the representation of place in the primate hippocampus. *Hippocampus, 9*(4), 467-480. https://doi.org/10.1002/(SICI)1098-1063(1999)9:4<467::AID-HIPO13>3.0.CO;2-F

Rolls, E. T. (2023). Hippocampal spatial view cells, place cells, and concept cells: View representations. *Hippocampus, 33*(5), 667-687. https://doi.org/10.1002/hipo.23536

Sharp, P., Kubie, J., & Muller, R. (1990). Firing properties of hippocampal neurons in a visually symmetrical environment: Contributions of multiple sensory cues and mnemonic processes. *The Journal of Neuroscience, 10*(9), 3093-3105. https://doi.org/10.1523/jneurosci.10-09-03093.1990

Sinclair, A. H., Manalili, G. M., Brunec, I. K., Adcock, R. A., & Barense, M. D. (2021). Prediction errors disrupt hippocampal representations and update episodic memories. *Proceedings of the National Academy of Sciences - PNAS, 118*(51) https://doi.org/10.1073/pnas.2117625118

Simons, D. J., & Wang, R. F. (1998). Perceiving real-world viewpoint changes. *Psychological Science, 9*, 315-320.

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 the United States of America, 108*(3), 1152–1157. http://doi.org/10.1073/pnas.1011843108

Wang, R. F., & Brockmole, J. R. (2003). Human navigation in nested environments. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 29*(3), 398–404. https://doi.org/10.1037/0278-7393.29.3.398

Wang, R. F., & Spelke, E. S. (2000). Updating egocentric representations in human navigation. *Cognition, 77,* 215-250.

Wang, R. F., & Simons, D. J. (1999). Active and passive scene recognition across views. *Cognition, 70*(2), 191-210. https://doi.org/10.1016/S0010-0277(99)00012-8

Wang, R. F., Crowell, J. A., Simons, D. J., Irwin, D. E., Kramer, A. F., Ambinder, M. S., ... & Hsieh, B. B. (2006). Spatial updating relies on an egocentric representation of space: Effects of the number of objects. *Psychonomic bulletin & review, 13*, 281-286.

Wolbers, T., & Hegarty, M. (2010). What determines our navigational abilities? *Trends in Cognitive Sciences, 14*(3), 138-146.

Zhang, H., Mou, W., & McNamara, T. P. (2011). Spatial updating according to a fixed reference direction of a briefly viewed layout. *Cognition, 119*(3), 419-429. https://doi.org/10.1016/j.cognition.2011.02.006

Zhang, L., & Mou, W. (2017). Piloting systems reset path integration systems during position estimation. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 43*(3), 472-491. https://doi.org/10.1037/xlm0000324

Zhang, L., & Mou, W. (2019). Selective resetting position and heading estimations while driving in a large-scale immersive virtual environment. *Experimental Brain Research, 237*(2), 335-350. https://doi.org/10.1007/s00221-018-5417-x

Zhang, L., Mou, W., Lei, X., & Du, Y. (2020). Cue combination used to update the navigator's self-localization, not the home location. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 46*(12), 2314-2339. https://doi.org/10.1037/xlm0000794

Zhao, M., & Warren, W. H. (2015a). Environmental stability modulates the role of path integration in human navigation. *Cognition, 142,* 96-109. https://doi.org/10.1016/j.cognition.2015.05.008

Zhao, M., & Warren, W. H. (2015b). How you get there from here: Interaction of visual landmarks and path integration in human navigation. *Psychological Science, 26*(6), 915-924. https://doi.org/10.1177/0956797615574952