Path integration, rather than being suppressed, used to update spatial views in familiar environments with landmarks always available

by

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Abstract

This project, following the elegant paradigm developed by Zhao and Warren (2015b), investigated how self-motion cues and landmarks are used during navigation in a familiar environment with constantly available landmarks. Participants learned the location of a specific object. After completing one outbound path starting from the object, participants pointed to the object (homing). In Experiments 1 and 1b, there were landmarks throughout the first 9 trials. On some later trials, the landmarks were presented during the outbound path but unexpectedly removed during homing (catch trials). On the last trials, there were no landmarks throughout (baseline trials). Experiments 2-3 were similar but added two identical objects (the original one and the distractor one that was rotated from the original one) during homing on the catch and baseline trials. Experiment 4 added two groups of landmarks (the original and the rotated distractor) instead of two targets. The results showed homing angular error on the first catch trial was significantly larger than the matched baseline trial in Experiments 1 and 1b. In contrast, the proportion of participants who correctly recognized the original object or landmarks was comparable on the first catch and the matched baseline trial in Experiment 2-4. These results indicated that self-motion cues might be used to update spatial views of the familiar environment during locomotion. Although an unexpected removal of landmarks creates mismatches between updated and real views, impairing homing performance, the updated spatial views can remove the ambiguous targets or landmarks in the familiar environment.

Keywords: path integration, piloting, homing, landmark recognition, spatial views

Preface

This thesis is an original work by Yue Chen. The experiments in this thesis received research ethics approval from the University of Alberta Research Ethics Board, Project Name "Human spatial cognition", No. Pro00082900.

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1. Introduction

In spatial navigation, people need to localize themselves and important goals in the environment, relying on multiple sources of spatial information (Cheng et al., 2007). Generally, spatial information can be divided into two categories: visual landmarks and self-motion cues (e.g., vestibular, proprioceptive, motor efference copy, and optic flow) (Newman et al., in press). The process of using landmarks is referred to as piloting, while the process of using self-motion cues is referred to as path integration (Cheng & Spetch, 1998; Etienne et al., 2004; Foo et al., 2005; Gallistel & Matzel, 2013; Loomis et al., 1999; Mittelstaedt & Mittelstaedt, 1980; Wang, 2017; Wehner et al., 1996). For example, we can find out our way to the bathroom in our house at night without turning on the lights, which indicates the function of path integration. We can reach the building by seeing a familiar logo on the building when we exit a subway station, which indicates the function of piloting. Clear empirical evidence indicates that either piloting or path integration could alone guide spatial localization (Cheng, 1986; Doeller & Burgess, 2008; Rieser, 1989, 1999; Huffman & Ekstrom, 2019; see Mou & Qi, in press for a review). However, it is not clear how these two processes jointly guide our localization.

Research over the past decade has suggested that path integration and piloting are independent (Chen et al., 2019; Chen et al., 2017; Nardini et al., 2008; Sjolund et al., 2018; Zhang & Mou, 2017; Zhang et al., 2020). There are two lines of evidence. First, when both cues were available, participants appeared to combine estimates based on single cues in the optimal/Bayesian manner (Chen et al., 2019; Chen et al., 2017; Nardini et al., 2008; Sjolund et al., 2018). In a typical paradigm, participants walk an outbound path with both self-motion and landmark cues and then return/point to the origin of the outbound path (homing). During the homing phase, there are only self-motion cues, landmark cues, or both cues (consistent or conflicting) across different trials. The primary findings showed that participants' variance in the accuracy of homing behavior (i.e., homing variance) in both cues condition was reduced, compared to the variance in single cues condition, and the degree of reduction can be predicted by the optimal/Bayesian cue combination (e.g., Nardini et al., 2008). As the optimal/Bayesian cue combination assumes independent estimates from single cues (Ernst & Banks, 2002; Ma, 2019; Zhang et al., 2020), the observed optimal/Bayesian cue combination suggests independence of piloting and path integration.

Second, there is no evidence of cue overshadowing between these two processes (Chen et al., 2017; Newman & McNamara, 2020; but see Zhao & Warren, 2015b). Cue competition is a phenomenon where the spatial learning of cue A is impaired by simultaneous spatial learning of cue B, indicating that learning cue A may share the same resources used in learning cue B (Doeller & Burgess, 2008; Mou & Spetch, 2013). Conversely, no cue overshadowing suggests independence between spatial learning processes of cue A and cue B (Cheng, 2008). Chen and her colleagues (2017) showed that the homing variance based on each cue (e.g., the landmark cue) could be manipulated by varying the cue quality of that specific cue (e.g., change the number of the landmarks). However, while the homing variance based on one cue changed with the quality of that cue, the homing variance based on the other cue (e.g., self-motion) did not change, indicating varying the quality of one cue has no effect on the estimate variance based solely on the other cue. Newman and McNamara (2020) reported that presenting only one cue or two cues during the outbound path did not affect homing variance on either cue, also indicating no cue overshadowing between piloting and path integration (see also Shettleworth & Sutton, 2005 for similar results in rats).

In addition to the finding of the independent estimates of spatial locations from piloting and path integration, research in the past decade also suggests that people integrate these independent estimates after the outbound path rather than during the outbound path (Mou & Zhang, 2014; Zhang & Mou, 2017; see also Mou & Qi, in press; Newman et al., in press for reviews). In Mou and Zhang (2014), participants learned the locations of several objects with the presence of distal landmarks, which were very far away and provided only orientation information. Participants walked an outbound path with two legs and one turn and then indicated the objects' original locations. The distal landmarks and objects were removed when participants walked the first leg. As a manipulation, the distal landmarks reappeared when participants walked the second leg but disappeared again during the homing phase, or reappeared when participants completed the outbound path and remained there during the homing phase. The results showed that participants' orientation was determined by the rotated distal landmarks when they saw the rotated landmarks during the homing phase, whereas their orientation was determined by the self-motion cues when they saw the rotated landmarks during the outbound path. This result indicates that participants only compared the separate orientation estimates based on self-motion or based on the rotated landmarks during the homing phase, but ignored the rotated landmarks during the outbound path. Similarly, Zhang and Mou (2017) showed that participants' position was determined by a displaced proximal landmark when they saw the landmark during the homing phase, whereas their position was determined by the self-motion cues when they saw the displaced proximal landmark during the outbound path. Again, participants ignored the displaced landmark during locomotion. These results suggest that cue integration between self-motion cues and landmarks might not occur during the outbound path but rather after it.

The conclusions that path integration and piloting are independent and cue interaction occurs during the homing phase but not during the outbound path are consistent with a general belief in the broader literature of human and animal spatial cognition (Cheng et al., 2007; Gallistel, 1990; Goodridge & Taube, 1995; Müller & Wehner, 1988). According to this belief, path integration is an automatic and dynamic process that is always active. In contrast, piloting is an intermittent process since landmarks are not always available. Piloting resets path integration as errors accumulate during path integration (Etienne & Jeffery, 2004; but see Tcheang et al., 2011).

The paradigms used to study cue interaction typically do not involve constantly available landmarks. In these paradigms, participants saw a removal of landmarks in the self-motion cue only condition or they encountered a landmark that had been rotated or displaced in the conflict cue condition (e.g., Nardini et al., 2008; Chen et al., 2017). This design might encourage participants to primarily rely on path integration during the outbound path. However, in a familiar environment, people may always see landmarks. For example, in our homes, we can always see familiar furniture in different rooms as we move around. It is not clear whether the findings from environments where landmarks were not always available can be generalized to a familiar environment with constantly available landmarks. Therefore, since we often navigate familiar environments in everyday life, it is important to systematically investigate how piloting and path integration jointly guide our localization in a familiar environment with constantly available landmarks.

The current study proposes three hypotheses to examine the cue interaction in a familiar environment with constantly available landmarks. The first hypothesis posits that the principle of cue interaction is independent of the type of environment. Regardless of whether landmarks are constantly available or not, path integration and piloting are independent and cue interaction occurs during the homing phase but not during the outbound path. This hypothesis is consistent with the general belief that path integration is automatic and always functioning during locomotion (Chen et al., 2019; Cheng et al., 2007; Etienne & Jeffery, 2004; Gallistel, 1990; Zhang & Mou, 2017). We refer to this hypothesis as the environment-free hypothesis.

The second hypothesis stipulates that when landmarks are constantly available, path integration is suppressed (e.g., Zhao & Warren, 2015b). According to this hypothesis, people rely on path integration during locomotion in an environment where landmarks might not be constantly available but suppress path integration during locomotion in an environment where landmarks are always available. Intuitively, this hypothesis makes perfect sense. Landmarks are dominant over path integration (Etienne & Jeffery, 2004; Foo et al., 2005; Mou & Zhang, 2014; Zhang & Mou, 2017). Thus, estimates from path integration is useless if they are always overridden by landmarks that are constantly available. Moreover, individuals' cognitive resources are limited. It would waste precious cognitive resources if people relied on path integration in an environment where landmarks are constantly available. Hence, the suppression of path integration is consistent with cognitive economy. We refer to this hypothesis as the suppression hypothesis.

The third hypothesis proposes that in environments with constantly available landmarks, path integration is utilized to update the spatial views of the environment. As people move around, they can predict the expected spatial views from changes in their position and orientation. Rolls (2008) reported that spatial view cells in the primate hippocampus respond not only to the actual view of the surrounding environment but also to the predicted views updated from path integration, even when the real view was obstructed by a curtain. This indicates that the cell is sensitive to the predicted spatial view updated from path integration.

We note that the updated spatial views are different from both the self-motion cue and the landmark cue. While the landmarks used in piloting are the real views, what is actually seen, the updated spatial views are predicted imagery. In addition, the updated spatial views differ from self-motion cues because they associate predicted views with self-motion cues. Hence, the updated spatial view can be considered an integrated representation of self-motion and landmark cues (Chen et al., 2022; Du et al., 2020; Loomis et al., 2013; Rieser, 1999; Tcheang et al., 2011). In this integrated representation, the predicted view (imagery), compared to self-motion cues, might be the dominant component (Du et al., 2020; Rieser, 1999).

Different from the proposal of the suppression hypothesis that path integration is useless when landmarks are always available, spatial views updated from path integration can facilitate the process of piloting. Research has shown that recognizing a scene from a new viewpoint can be challenging, but this challenge can be eased by self-motion cues (Simons & Wang, 1998; Wang & Simons, 1999; Zhang et al., 2011). More critically, there could be identical landmarks in the same environment, which may provide ambiguous piloting information. For example, a goal location might be indicated by a landmark, but there could be multiple identical landmarks at different locations. In such cases, updating spatial views can help remove the spatial ambiguity (Etienne et al., 1998; Lee et al., 2006; Sharp et al., 1990). We refer to the third hypothesis as the updating-spatial-views hypothesis.

To the best of our knowledge, Zhao and Warren (2015b) conducted the first and the only study to shed light on how piloting and path integration jointly guide our localization in a familiar environment with constantly available landmarks. In their Experiment 1, they used a very elegant design where participants navigated in a familiar environment with constantly available landmarks, but the landmarks were suddenly removed during homing on a critical testing trial. In particular, on a standard trial, with landmarks available throughout, participants viewed the location of the home and walked to the home (learning phase), then walked the outbound path with two legs from the home (outbound phase), and at last returned to the home (homing phase). Participants had plenty of standard trials to develop the expectation of seeing the constantly available landmarks during the homing phase. After that, on a catch trial, participants still saw landmarks during learning and outbound phases but not during the homing phase, where the landmarks had been unexpectedly removed. As a comparison, on the baseline trials that were presented after the catch trials, participants never saw any landmarks throughout the trial. The results showed that the absolute mean homing error on the first catch trial was significantly larger than the absolute mean homing error on the matched path baseline trial. However, this different disappeared for the following catch trials and matched path baseline trials.

The results of worse homing performance on the first catch trial in Zhao and Warren's (2015b) Experiment 1 indicate that path integration seems to operate differently depending on whether participants expected they would always see the landmarks during homing or not. As the environment-free hypothesis indicates that path integration should operate similarly whether there are always landmarks in the environment or not, the environment-free hypothesis is undermined. However, it is not clear from Zhao and Warren's (2015b) study whether their results support the suppression hypothesis or the updating-spatial-views hypothesis. Both hypotheses suggest that the absence of landmarks during homing would affect path integration, but the mechanisms underlying this effect differ. Therefore, further research is needed to distinguish between the suppression hypothesis and the updating-spatial-views hypothesis.

The suppression hypothesis readily explains the result of the impaired homing performance on the first catch trial. According to this hypothesis, participants rely solely on visual landmarks to navigate in a familiar environment. The function of path integration is suppressed during the outbound path if they believe that the visual cues are reliable. Therefore, path integration was impaired on the first catch trial, where participants expected to see landmarks during homing but in fact did not. In contrast, path integration was not impaired on the baseline trials, where there were no landmarks throughout the trial. Hence, homing performance was worse on the first catch trial than the matched path baseline trial.

The updating-spatial-views hypothesis can also explain the impaired homing performance on the first catch trial. This hypothesis suggests that participants use path integration to update the spatial views of the environment, and unexpected removal of visual landmarks causes a mismatch between the predicted and real views. Since views are dominant over self-motion cues (Collett & Collett, 2000), view mismatch could disrupt the self-motion representations (via a mechanism like reset by a real view of the empty scene). Therefore, the unexpected removal of visual landmarks disrupted self-motion representations and then impaired homing performance based solely on self-motion cues on the first catch trial. By contrast, on the baseline trials, as participants did not see the landmarks at all, there was no view mismatch. Therefore, no impairment was expected during the homing phase. Hence, homing performance was worse on the first catch trial than on the matched path baseline trial.

The current study aimed to investigate the roles of the path integration in a familiar environment with constantly available landmarks by testing the three hypotheses. Experiments 1 and 1b were conducted to differentiate the environment-free hypothesis from the other hypotheses. We acknowledge that the results of Zhao and Warren's Experiment 1 (2015b) have already undermined the environment-free hypothesis. However, surprisingly, no other study has been conducted to replicate the important results of Zhao and Warren's Experiment 1 (2015b).

Furthermore, the environment-free hypothesis is based on the general belief that path integration is an automatic and dynamic process, always active and independent of piloting (Cheng et al., 2007; Etienne & Jeffery, 2004; Gallistel & Matzel, 2013). Therefore, replication of Zhao and Warren's Experiment 1 was still required before we totally discarded the environment-free hypothesis. Experiment 1 and 1b replicated Zhao and Warren's Experiment 1 (2015b).

Experiments 2 to 4 were designed to distinguish between the suppression hypothesis and the updating-spatial-views hypothesis, by presenting ambiguous target objects or landmarks instead of the empty scene during the homing phase on the first catch trial. In Experiments 2 and 3, we presented two identical target objects, one at the original home location and the other at a distractor location that was rotated from the origin home. In Experiments 4, during the homing phase on the first catch trial, we presented two groups of landmarks: the original group and the distractor group that was rotated from the original group. According to the updating-spatial-views hypothesis, the updated spatial views could be used to remove visual ambiguity and distinguish the correct target or landmarks from the distractor ones. In addition, the recognized target or landmarks could be helpful to homing. Therefore, there would be no impairment on the first catch trial compared to the matched path baseline trial. In contrast, the suppression hypothesis still predicts impairment on the first catch trial because path integration would be suppressed during the outbound path of the first catch trial and could not be used to recognize the correct target or landmarks.

2. Experiment 1

The purpose of Experiment 1 was to replicate the finding of Zhao and Warren's (2015b) experiment 1. To our best knowledge, no studies have been conducted to replicate this important finding. On each trial, in an immersive environment, participants viewed a home location from the start location and then walked to the home location (learning phase; see Figure 1a S→O). Participants then walked an outbound path with two legs (outbound phase; see Figure 1a O→T→P). After completing the outbound path, participants indicated the home location (homing phase; see Figure 1a P→O). The presence of visual information was manipulated across different conditions (See supplementary Table S1 for details). On standard trials, the visual landmarks were always visible at the fixed locations throughout the trial. On catch trials, the visual landmarks were presented during the learning and outbound phases but removed unexpectedly before the homing phase. On baseline trials, there were no visual landmarks throughout the trial. There were at least nine standard trials before the first catch trial so that participants would have developed an expectation of seeing the visual landmarks at the fixed locations during the homing phase. Following Zhao and Warren's (2015b) experiment 1, we predicted that the homing angular errors on the first catch trials would be significantly larger than the homing angular errors on the first baseline trials, but the homing angular errors on the later catch trials might be comparable to those on their matched baseline trials.

2.1 Method

2.1.1 Participants

The study was approved by the Ethics Committee of the University of Alberta. Twenty-four university students (12 females, 12 males) with normal or corrected-to-normal vision participated as partial fulfillment of a requirement for their introductory psychology courses at the University of Alberta. All participants provided consent to participate in this experiment.

Based on the effect size (Cohen's $dz = 1.39$) of the difference between the first catch and baseline trials in Experiment 1 of Zhao and Warren's (2015b, p. 101), a sample size of 24 participants would achieve a power of 0.999 in observing a significant difference in the homing errors between the first catch and baseline trials using a two-tailed paired t-test at an alpha level of .05.

2.1.2 Materials and Design

The real experimental room was 4.4 x 4.4 metres large. An immersive virtual environment was generated by Vizard software (WorldViz, Santa Barbara, CA) and presented to participants via a head-mounted display (HMD, Oculus Rift, Oculus VR, LLC., Irvine, CA). Head motion tracking was carried out by an InterSense IS-900 motion tracking system (InterSense, Inc., Massachusetts). Participants indicated the home location by pointing with a virtual stick, which they controlled using head movements. The virtual stick was originated from the head motion tracker and pointing to participants' head facing direction. The response home location was indicated by the intersection between the virtual stick on the ground surface. The virtual stick was only visible when participants needed to point to home. Participants were asked to move their heads to align the virtual stick with the direction that they wished to point and pressed the button on a head-held remote to confirm their responses. Once participants confirmed their response, the virtual stick disappeared to avoid blocking the view.

Participants physically walked and made turns to move in the real lab space, but they never saw the real lab space. For each trial, there was a start point (S in Figure 1a) and a path consisting of three points: origin, turning point, and testing position (O, T, and P in Figure 1a). The outbound walking path (i.e., O-T-P) was marked by 2-metre-tall colored poles that were presented one at a time in a fixed order (i.e., red - red - green) (see an example of a red pole in Figure 1b). There were 12 different paths (see Figure 1c), having different origins (O) but sharing the same turning point (T) and testing position (P). The lengths of O-T and T-P were fixed to be 1.2 metres. The 12 possible origins (O) rested on a circle, centered on T with a radius of 1.2 metres. The turning angle varied between 35° and 110° clockwise or countclockwise. Across trials, the start location was fixed and marked by using a red arrow on the ground. The red arrow faced the first red pole for each specific trial.

Three distinctive 2-metre-tall towers, resembling the Eiffel tower, Big Ben, and TV Tower (in Figure 1b), served as proximal landmarks. These towers were placed 5 metres from the testing position (P). The middle tower was located on the same axis as the start point (S) and the testing position (P), while the other two towers were 45° apart from the middle tower. Their locations remained constant throughout the experiment.

There were three types of trials. On standard trials, the landmarks were visible throughout the trial. On catch trials, the landmarks were only visible before the homing phase. On baseline trials, no visual landmarks were visible throughout the trial. In total, there were 24 trials. The first nine trials were always the standard trials (also referred to as familiarity trials in the result section), followed by a mixture of another nine standard trials and three catch trials. There at least one standard trials between two catch trials. The last three trials were the baseline trials. For each participant, nine of the twelve paths (Figure 1c) were randomly selected and assigned to the standard trials (each path was used twice as there were 18 standard trials in total). The other three paths were assigned to the three catch trials and the three baseline trials. The paths used on the catch trials and baseline trials were matched according to their trial order (e.g., the same path was used on the first catch and first baseline trials).

The dependent variable was the absolute angular error of homing direction, the angular difference between the correct homing direction (from P to O) and participants' response of the homing direction.

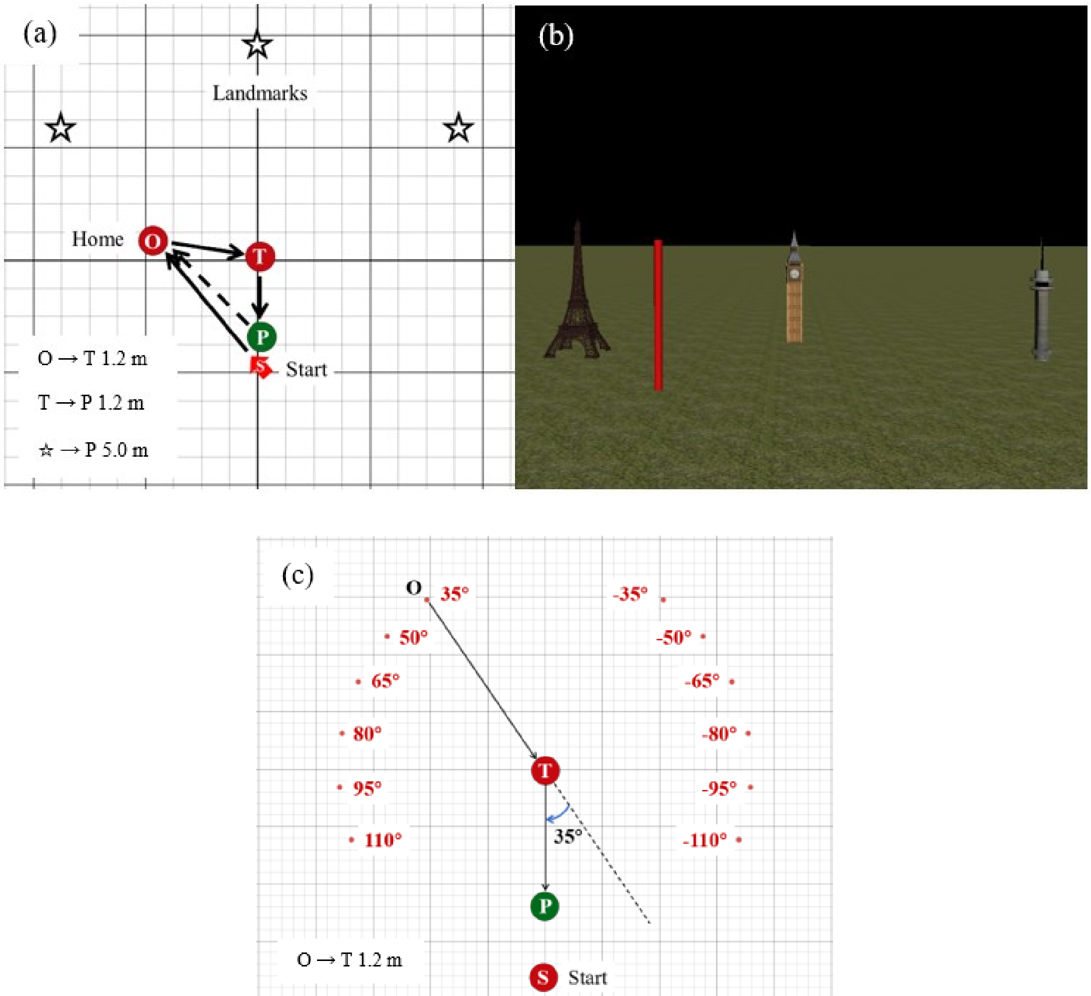


Figure 1. (a) Schematic experimental setup in Experiment 1. The stars represent the locations of three landmarks. S represents the start location; O represents the home location; T represents the turning point; P represents the testing location. Thus O-T-P is the outbound path. The dash arrow line (P-O) represents the correct homing vector. (b) A screenshot of the virtual environment with three visual landmarks; the red pole denotes the home location (O). (c) Twelve possible home locations and outbound paths. The turning angle of outbound paths varied between 35° and 110° (positive values for the clockwise turning direction).

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 guided the participants to the virtual environment room by holding their wrist. The participants kept their eyes closed until the experimenter placed the HMD on their head. White noise was played through the HMD earphones to reduce any orientation cues from the sounds in the real environment.

In addition to the virtual environment, participants received instructions displayed on the HMD at times. Following instructions, participants looked for a red arrow on the ground (at S in Figure 1a), walked towards it, and aligned themselves with its direction. The first red pole (at O in Figure 1a) then appeared in front of the participants, together with the three towers. Participants were given 10 seconds to remember the location of the first red pole. They were then instructed to walk towards the red pole. When the participant reached it, the first red pole disappeared. The second red pole (at T in Figure 1a) appeared, and participants were asked to face and walk towards it. They were asked to turn their body slowly until they could see the second red pole. When the participant reached it, the second red pole disappeared. The same procedure was followed to reach the green pole (at P in Figure 1a). When the participants reached the green pole, their view of the virtual environment was blocked for 8 seconds (i.e., a short duration of blackout). When the participants could see the environment again, they were instructed to turn their body around and point to the original location of the first red pole (O). Specifically, the virtual stick appeared. The participants were asked to move their head to align the virtual stick with the home location and then press a button on a hand-held remote to confirm their response. After confirmation, their pointing direction was recorded. All visual items, except for the grass field, were then removed, and participants were led to a random location with their eyes closed. The red arrow appeared again to indicate the start position (S), and the next trial began.

The procedure for the three conditions was identical, except for the following differences: on standard trials, landmarks appeared when participants reached the start position (S) and remained visible throughout the trial; on catch trials, landmarks appeared when participants reached the start position and disappeared after participants reached the green pole (P); and on baseline trials, landmarks were never presented.

2.1.4 Data Analysis

For each trial, the absolute homing error was calculated. The mean absolute homing error in each trial condition was calculated for each participant. The mean absolute homing error across different conditions were compared using repeated measure ANOVAs with one within-participant variable (i.e., condition) using JASP (JASP Team (2023). JASP (Version 0.17.1) [Windows 11]). As we were primarily interested in comparing the performance on the catch trials and the corresponding baseline trials, especially the first catch and baseline trials, we conducted paired t-tests to compare the matched catch and baseline trials. To qualify any null effect, we also calculated the Bayes factor favoring the null effect over the alternative effect (BF_{01}) using JASP (JASP Team (2023). JASP (Version 0.17.1) [Windows 11]). To distinguish the first 9 standard trials from the second 9 standard trials, we referred to the first 9 standard trials as familiarity trials and the second 9 standard trials as 9+ standard trials.

2.2 Results

Figure 2a shows the overall mean absolute homing error for each condition. Homing error did not significantly differ between the familiarity trials and the 9+ standard trials, $t(23) = 0.103$, $p = .919$, Cohen's $dz = 0.021$, $BF_{01} = 4.636$. We compared the mean absolute error among the all

18 standard trials (all standard trials in Figure 2a), the catch trials, and the baseline trials. The main effect of condition was significant, $F(2, 46) = 12.199$, $p < .001$, $MSE = 1199.593$, $\eta_p^2 = .347$. The main effect was still significant after the Huynh-Feldt correction (ε =.842), $F(1.684, 38.740) = 12.199$, $p < .001$. Post-hoc testing using Bonferroni correction revealed the following significant differences: the homing error was significantly larger in the catch trial condition than in the baseline trial condition (mean difference = 8.587, $p = .042$, Cohen's $dz = 0.800$) and the standard trial condition (mean difference = 14.022, $p <.001$, Cohen's $dz = 1.306$). Moreover, homing error in the baseline trial condition was significantly greater than the standard trial condition (mean difference = 5.435, $p = .037$, Cohen's $dz = 0.506$).

Figure 2b illustrates the absolute homing error of each catch trial and its matched baseline trial. Homing error was significantly larger on the first catch trial than on the first baseline trial, $t(23) = 2.202$, $p =.038$, Cohen's $dz = 0.450$, $BF_{01} = 0.617$. This disappeared for the following catch and matched baseline trials, $t(23) = 0.860$, $p = .399$, Cohen's $dz = 0.175$, $BF_{01} = 3.338$; $t(23) = 1.911$, $p = .069$, Cohen's $dz = 0.390$, $BF_{01} = 0.983$ for the second and third trials respectively.

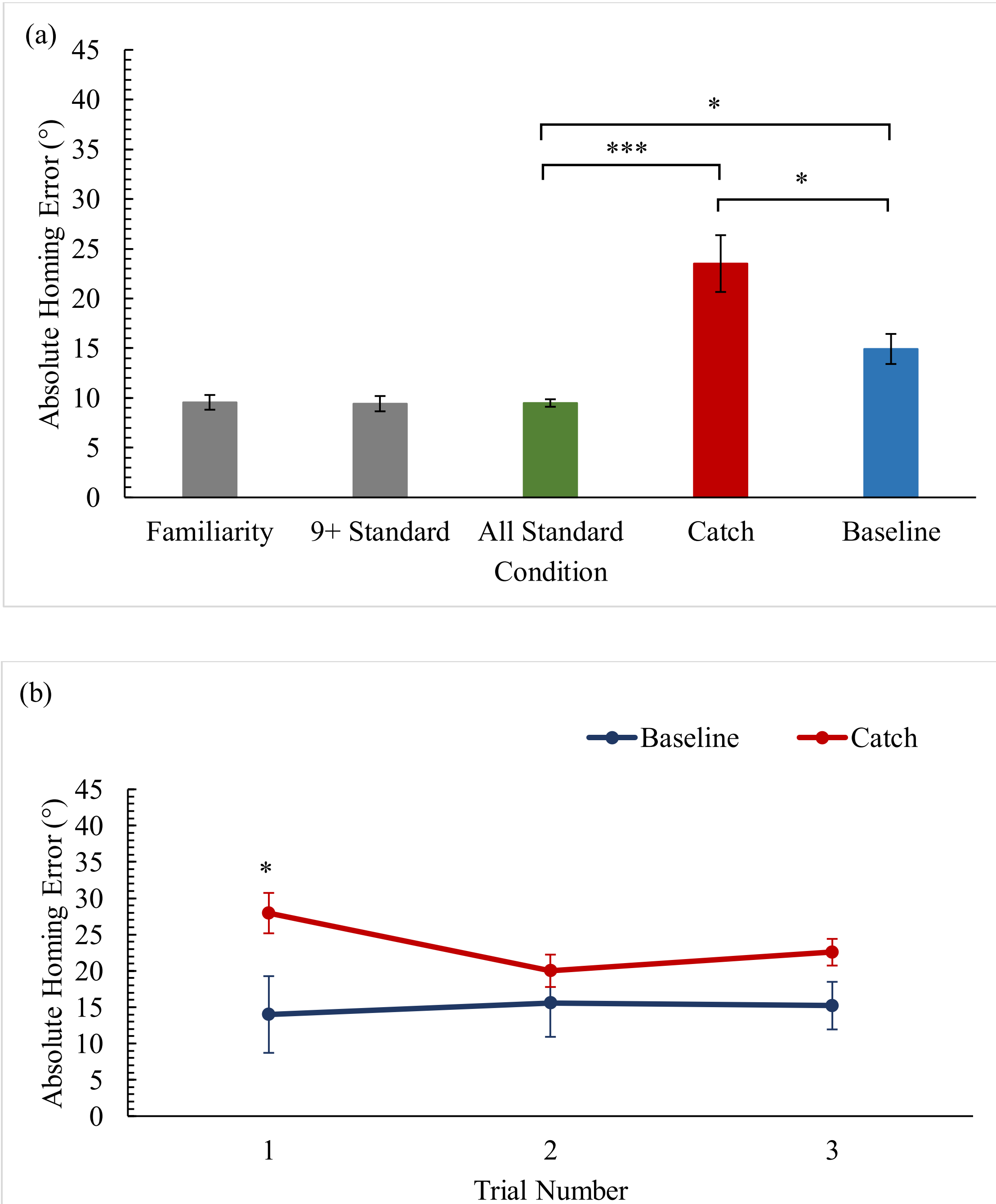


Figure 2. *(a) Absolute homing error for each condition in Experiment 1. (b) Absolute homing error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 3rd) in Experiment 1. The error bar was calculated*

by removing the error due to individual differences from the standard error of each trial.

2.3 Discussion

Experiment 1 replicated the key findings of Zhao and Warren's Experiment 1 (2015b), demonstrating that homing error was larger for the first catch trial than for the first baseline trial, but this difference disappeared for the second and third catch and baseline trials. However, the observed difference between the first catch trial and the first baseline trial in the current experiment, although significant, appeared to be obviously smaller than that reported by Zhao and Warren's Experiment 1 (2015b). Specifically, the non-standardized difference was 14° in the current study, compared to 60° in Zhao and Warren's Experiment 1 (2015b). Similarly, Cohen's $dz = 0.45$ in the current study, but Cohen's $dz = 1.39$ in Zhao and Warren's Experiment 1 (2015b).

Due to the smaller effect size observed in the current experiment, we were concerned that the significant effect might be attributed to a false positive error (type I error) rather than true replication of the finding from Zhao and Warren's Experiment 1 (2015b). To address this concern, we conducted a replication experiment, Experiment 1b, with one minor modification.

3. Experiment 1b

The purpose of Experiment 1b was to replicate the findings of Experiment 1. In Experiment 1, we asked participants to point to the location of the first red pole. However, the pole used in our experiment 1 was two metres high, which led to inconsistency in participants' responses as they could point to the top, middle, or bottom of the pole. To ensure that all participants pointed to the exact home location, we added a ball on the bottom of the first red pole (O), and participants were asked to point to the location of the ball. Otherwise, Experiment 1b is identical to Experiment 1.

3.1 Method

3.1.1 Participants

Twenty-four university students (12 females, 12 males) with normal or corrected-to-normal vision participated for credits in an introductory psychology course.

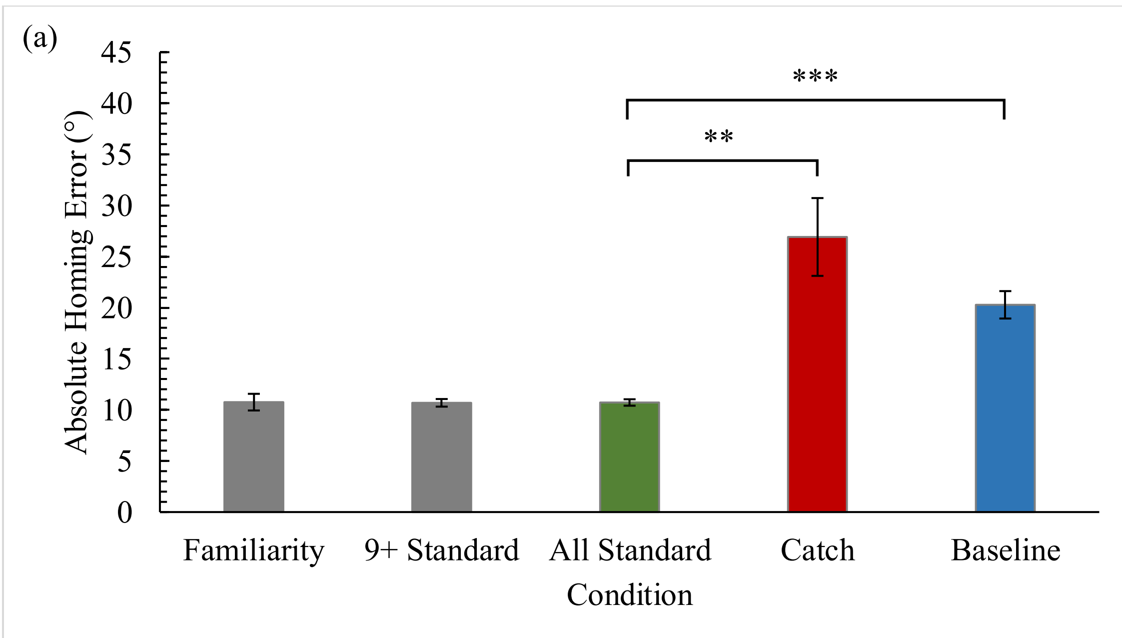
3.1.2 Materials, Design, and Procedure

The virtual environment in Experiment 1b was the same as in Experiment 1, with the addition of a ball (size of 0.04 m^3) placed on the ground under the first red pole (O) for each trial. Participants were explicitly instructed to learn the location of the ball during the learning phase. The ball disappeared when participants were instructed to walk towards the first red pole. In the homing phase, participants saw a smaller version of the ball floating on one corner of the HMD and were asked to indicate the original location of the ball by intersecting the virtual stick with the grassland.

3.2 Results

Figure 3a presents the overall performance for each condition. Homing error was not significantly different between the familiarity trials and the 9+ standard trials, $t(23) = 0.062$, $p = .951$, Cohen's $dz = 0.013$, $BF_{01} = 4.650$. We compared the homing error among three conditions including the all standard trial condition, the catch trials, and the baseline trials. The main effect of condition was significant, $F(2,46) = 10.168$, $p < .001$, $MSE = 1590.921$, $\eta_p^2 = .307$. The main effect of condition was still significant after the Greenhouse-Geisser correction (ε =.684), $F(1.367, 31.449) = 10.168$, $p = .001$. Post-hoc testing using Bonferroni correction revealed the following significant differences: the homing error was smaller in the standard trial condition than in the catch trial condition (mean difference = -16.196, $p = .003$, Cohen's $dz = -1.252$) and in the baseline trial condition (mean difference = -9.558, $p < .001$, Cohen's $dz = -0.739$).

Figure 3b illustrates the absolute homing error of each catch trial and its matched baseline trial. Homing error was larger for the first catch trial than for the first baseline trial, $t(23) = 2.569$, $p = .017$, Cohen's $dz = 0.524$, $BF_{01} = 0.324$. This difference disappeared for the following catch and matched baseline trials, $t(23) = -0.090$, $p = .929$, Cohen's $dz = -0.018$, $BF_{01} = 4.641$; $t(23) = 0.042$, $p = .967$, Cohen's $dz = 0.009$, $BF_{01} = 4.655$ for the second and third trials respectively.



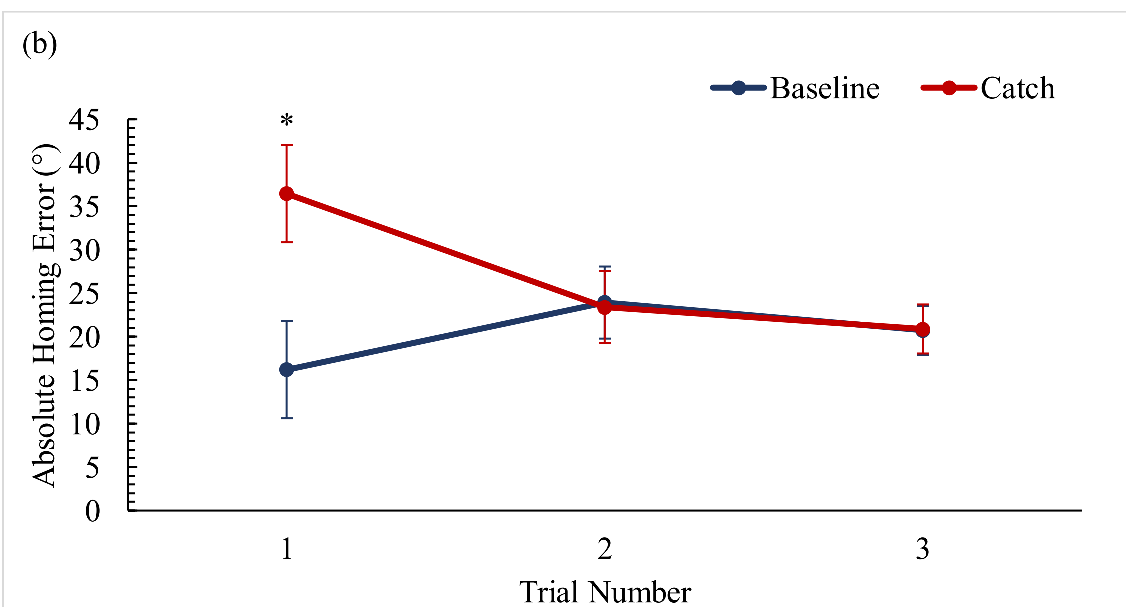


Figure 3. (a) Absolute homing error of each condition in Experiment 1b. (b) Absolute homing error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 3rd) in Experiment 1b. The error bar was calculated by removing the error due to individual differences from the standard error of each trial.

3.3 Discussion

As in Experiment 1, Experiment 1b still showed the homing error was significantly larger for the first catch trial than for the first baseline trial and this difference disappeared for the following catch and baseline trials. Thus, we are confident that Experiments 1 and 1b successfully replicated the important findings of Zhao and Warren's Experiment 1 (2015b) and provided evidence against the environmental-independent hypothesis. Consequently, Experiments 2-4 primarily tested the updating-spatial-views hypothesis and the suppression hypothesis.

4. Experiment 2

The main purpose of Experiment 2 was to differentiate the updating-spatial-views hypothesis from the suppression hypothesis. Experiment 2 was identical to Experiments 1b, except for the homing phase of the catch and baseline trials. While there was only grassland in Experiment 1b, two identical balls (target and distractor balls) were presented in Experiment 2. The target ball was presented at the original home location (O in Figure 1 (a)). The distractor ball was presented by rotating the target ball 65° around the participants who were standing at the testing position (i.e., P), clockwise or counterclockwise.

The suppression hypothesis predicts that participants still perform worse on the first catch trial than on the first baseline trial. Path integration is suppressed during the outbound path for the first catch trial, but not for the first baseline trial. As a result, participants are less likely discriminate the target ball from the distractor ball on the first catch trial than on the first baseline trial. Therefore, presenting two balls does not remove or reduce the homing error difference between the first catch and baseline trials. By contrast, the updating-spatial-views hypothesis predicts that participants update the spatial views of the environment through path integration during the outbound path. As suggested by the findings of Experiments 1 and 1b, the updated spatial views might be less useful in directly guiding homing on the first catch trial than on the first baseline trial. However, the updated spatial views are equally useful in distinguishing the target ball from the distractor ball on both the first catch and baseline trials. Thus, presenting two balls removes performance difference between the first catch and baseline trials.

The rotation angle between the target ball and the distractor ball should be carefully selected to differentiate the two hypotheses. The updating-spatial-views hypothesis predicts the same probability of recognizing the target ball for the first catch and baseline trials at all rotation angles. The suppression hypothesis might also predict the same probability of recognizing the target ball for the first catch and baseline trials when the rotation angle is too large or too small, producing a ceiling or floor effect. Hence, we should use a rotation angle at which the suppression hypothesis predicts a clearly lower probability of recognizing the target ball on the first catch trial than the first baseline trial.

Following the suppression hypothesis, we can calculate the predicted probability of recognizing the target ball for the first catch trial and for the first baseline trial using different rotation angles. We can then calculate the probability difference at each rotation angle. In particular, we assume that the remembered direction of the target ball is a normal distribution, $X \sim N(t, \sigma)$. t is the true direction of the target ball from the participants who are standing at the testing position (P). d is the direction of the distractor ball from the participants. r is the rotation angle ($r = d - t$)

(see Figure 4). The probability of choosing the target ball is the probability where the remembered direction (x) is closer to the true direction (t) than to the distractor direction (d). For a negative r (see Figure 4a), the probability of choosing the target ball is $P\ (X > t + \frac{r}{2})$. $P\ (X > t + \frac{r}{2})$ can be rewritten to be $P\ (Z > \frac{r}{2\sigma})$, where Z ~ N (0, 1). For a positive r (see Figure 4b), the probability of choosing the target ball is $P\ (X < t + \frac{r}{2})$ or $P\ (Z < \frac{r}{2\sigma})$.

We can also estimate σ, of the normal distribution of remembered ball direction, from the mean absolute homing error according to $\sigma = \sqrt{\frac{\pi}{3}}\, E(|x|)$, where $E(|x|)$ is the expectation of absolute homing error (Tsagris, Beneki & Hassani, 2014). E(|x|) can be estimated by the mean absolute homing error across trials and participants for each trial condition (M(|x|)). According to Experiment 1b (see Figure 3), for the first catch trial, M(|x|) was 36°, so σ_c= 45.12. For the first baseline trial, M(|x|) was 16°, so σ_b= 20.05. According to $P\ (Z > \frac{r}{2\sigma})$, Figure 4c illustrates the probability of choosing the target ball for the first catch trial and for the first baseline trial and probability difference between these trials at different rotation angles (-180,0).

We used a rotation angle of 65° in Experiment 2. While the updating-spatial-views hypothesis predicts a null probability difference, the suppressing hypothesis predicts that the probability difference between the first catch trial and the first baseline trial is 18% (see Rotation angle of -65° in Figure 4c).

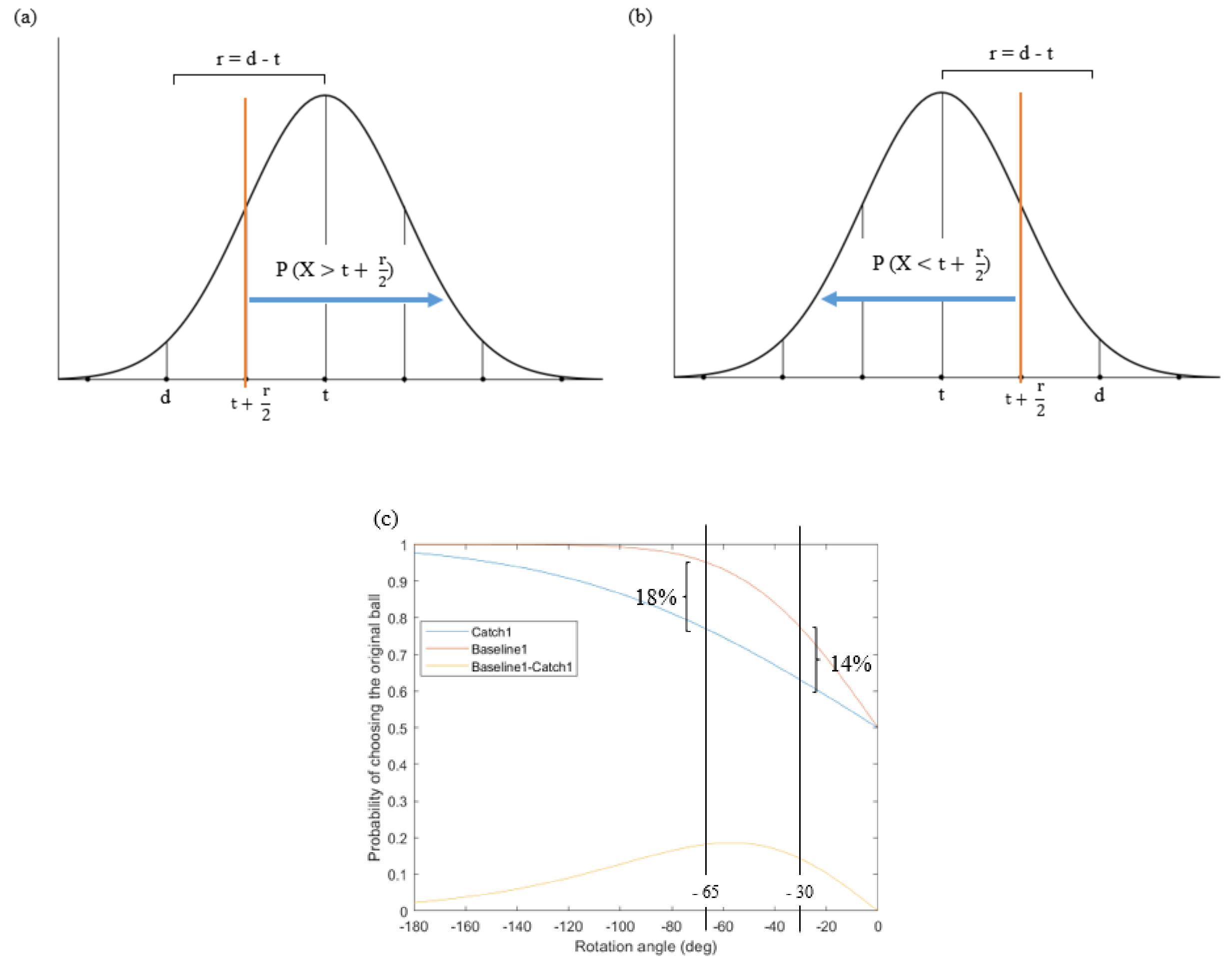


Figure 4. *(a and b) the probability of recognizing the target (t) from the distractor (d) is the probability where the remembered direction, which follows a normal distribution (X ~ N (t, σ)), is larger than the middle point between d and t (i.e.* $t + \frac{r}{2}$*) when d is smaller than t (panel a) or is smaller than* $t + \frac{r}{2}$ *when d is larger than t (panel b). (c) Probability of recognizing the target ball on the first catch and baseline trials and the probability difference between these two trials as a function of rotation angle according to the suppression hypothesis.*

4.1 Method

4.1.1 Participants

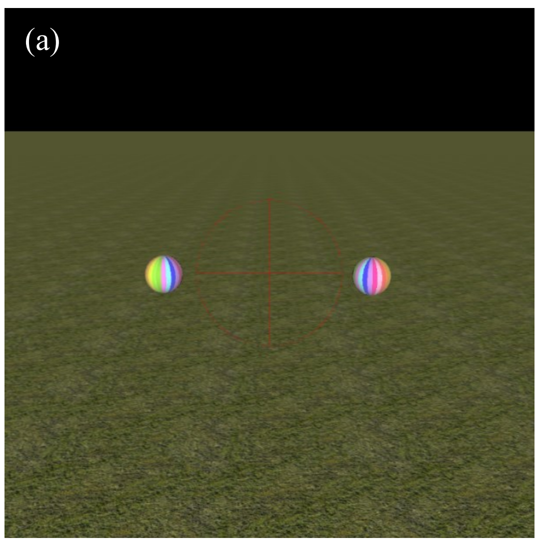
Forty-eight university students (24 females, 24 males) with normal or corrected-to-normal vision participated for credits in an introductory psychology course in Experiment 2.

We conducted a power analysis based on McNemar's test for proportion difference of paired nominal data. Participants were divided into four categories based on their correct or wrong responses on the first catch and baseline trials: those who are correct on both the first catch and baseline trials (referred to as category A), those who are correct on the first baseline trial but wrong on the first catch trial (referred to as category B), those who are correct on the first baseline trial but wrong on the first catch trial (referred to as Category C), and those who are wrong on both trials (referred to as Category D). The proportion of each group was labeled as p_a, p_b, p_c, and p_d respectively ($p_a+p_b+p_c+p_d=1$). p_a+p_b is the correct probability on the first baseline trial whereas p_a+p_c is the correct probability on the first catch trial. According to the suppression hypothesis, $(p_a+p_b) – (p_a+p_c) = 18\%$ (see Figure 4c for the rotation angle of -65°). Hence, we get $p_b - p_c =18\%$, which is the a priori proportion difference. Suppose the proportion of participants doing correct on one trial but wrong on the other trial (the proportion of discordant pairs, i.e., p_b+p_c) is low. Specifically, we assume $p_b+p_c =20\%$[1]. We get $p_b = 19\%$ and $p_c = 1\%$, and the odds ratio ($\frac{p_b}{p_c}$) =19. A sample size of 48 participants could achieve a power of 0.914 in observing the significant difference between p_b and p_c using a two-tailed paired McNemar's test at an alpha level of .05 (based on G*Power, Faul et al., 2009).

[1] This assumption was supported by the observed p_b+p_c in Experiments 2-4.

4.1.2 Materials, design, and procedure

Experiment 2 was identical to Experiment 1b with the following modification. During the homing phase of the catch trials and baseline trials, we presented two balls (the target ball and the distractor ball, see Figure 5a). The target ball was presented at the original home location, and the distractor ball was rotated 65° clockwise or counterclockwise from the target ball around the testing position (P). The rotation direction was chosen randomly across trials. Note that participants were not explicitly asked to choose the target ball. They were still asked to point to the original location of the ball as in Experiment 1b to make this experiment as comparable to Experiment 1b as possible.



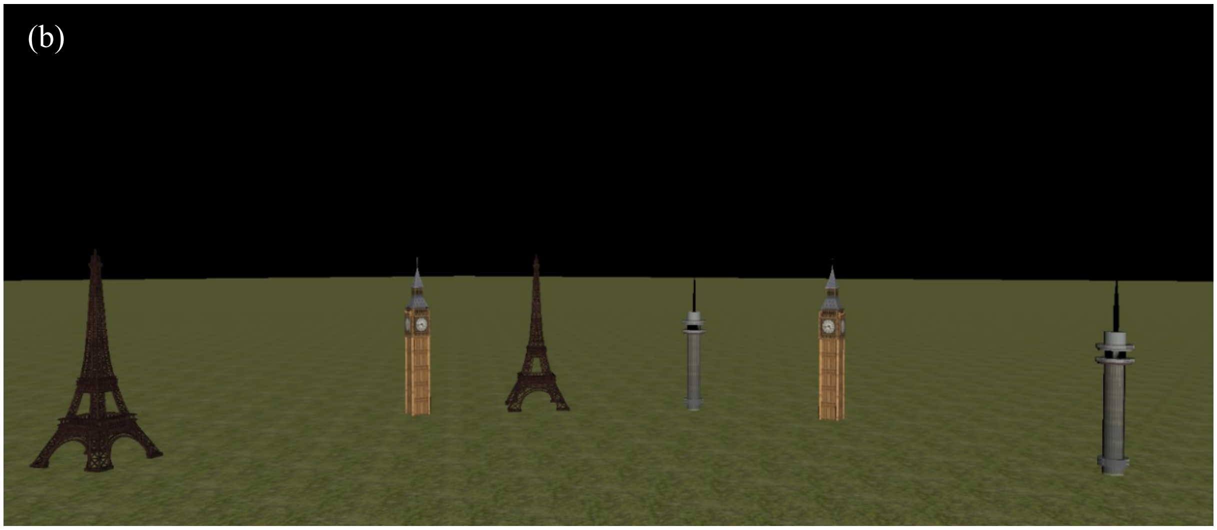


Figure 5. A screenshot of virtual environment during the homing phases of the catch and baseline trials for (a) Experiments 2 and (b) Experiment 4.

4.2 Results

4.2.1 Recognition performance

Because we did not ask participants to choose the target ball, we calculated the recognition performance based on each response of the homing direction. Correct recognition was determined if the response homing direction was closer to the target ball than to the distractor ball. Otherwise, wrong recognition was determined. Table 1 shows the distribution of participants in different categories of recognition performance. Among the 48 participants, 36 participants were correct for both the first catch and baseline trials (p_a=75.0%), 7 participants were correct for the first baseline trial but wrong for the first catch trial (p_b=14.6%), 4 participants were correct for the first catch trial but wrong for the first baseline trial (p_c=8.3%), and 1 participant was wrong for both the first catch and baseline trials (p_d=2.1%). Note that in power analysis, we assumed that p_b+p_c =20%. The observed p_b+p_c = 22.9%, is consistent with our assumption.

McNemar's test did not show any significant difference in the proportion of participants who recognized the target ball for the first catch and baseline trials (p_a+p_c=83.3% vs. p_a+p_b=89.6%), X^2 (1, N = 11) = 0.36, p = .546. To qualify the null effect, we also calculated the Bayes Factor to compare the null effect (i.e., $\frac{p_b}{p_b+p_c} = 0.5$) with the predicted effect of 18% (i.e., $\frac{p_b}{p_b+p_c} = 0.893$)[2]. The observed 7 participants in category B whereas 4 participants in category C, following a binomial distribution with a parameter ($\frac{p_b}{p_b+p_c}$) of 0.5 or 0.893, favored the null effect, BF_{01} = 8.15.

The results of the second and third catch and baseline trials were similar (see details in the supplementary materials).

Table 1

Proportion of participants in different categories of recognition outcomes on the first catch trial and the first baseline trial in Experiment 2.

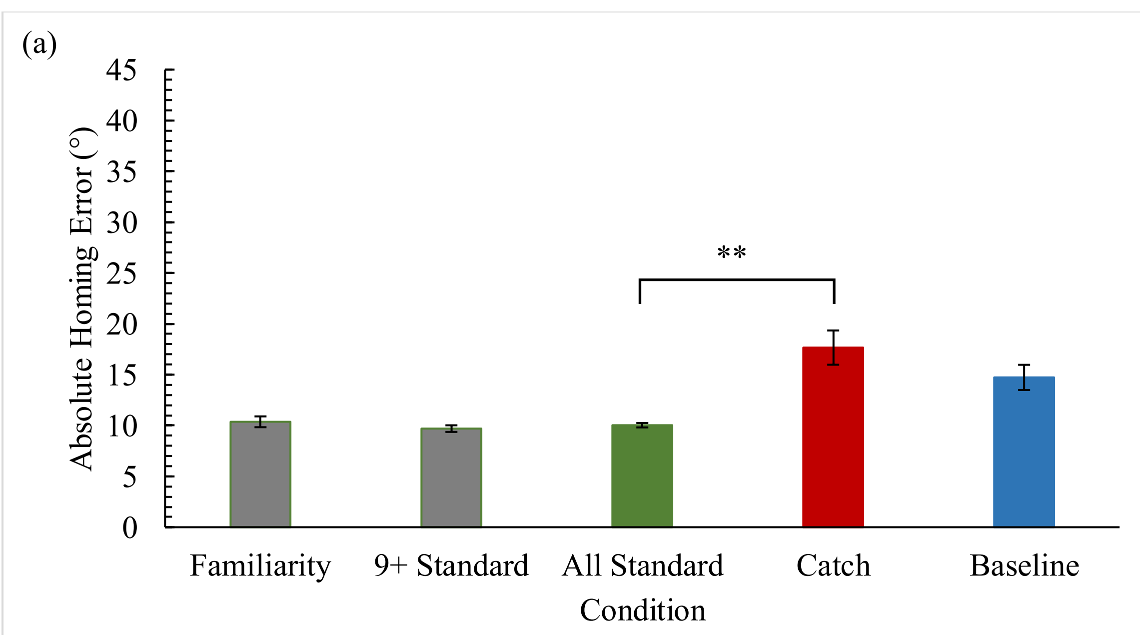
$p_a+p_b+p_c+p_d=1$		1st Catch Trial		
		Correct	Incorrect	
1st Baseline Trial	Correct	$p_a=\frac{36}{48}$ = 75.0%	$p_b=\frac{7}{48}$ = 14.6%	p_a+p_b= 89.6%
	Incorrect	$p_c=\frac{4}{48}$ = 8.3%	$p_d=\frac{1}{48}$ = 2.1%	
		p_a+p_c= 83.3%		

[2] Using the observed p_b+p_c = 22.9% and the predicted effect, p_b-p_c = 18%, we get predicted $\frac{p_b}{p_b+p_c} = 0.893$ for the alternative hypothesis.

4.2.2 Homing Errors

Figure 6a shows the overall performance for each condition. Homing error in the familiarity trials was not statistically different from the 9+ standard trials, $t(47) = 0.876$, $p = .385$, Cohen's $dz = 0.126$, $BF_{01} = 4.442$. The main effect of trial condition (all standard trials, catch trials, and baseline trials) was significant, $F(2,94) = 6.199$, $p = .003$, $MSE = 711.282$, $\eta_p^2 = .117$. Post-hoc testing using Bonferroni correction showed only one significant difference: the homing error was larger in the catch trial condition than in the standard trial condition (mean difference = 7.631, $p = .002$, Cohen's $dz = 0.581$).

Figure 6b illustrates the absolute homing error of each catch trial and its matched baseline trial. Homing error was not significantly different between the first catch trial and the first baseline trial, $t(47) = 1.236$, $p = .233$, Cohen's $dz = 0.178$, $BF_{01} = 3.123$. This pattern can also be found for the following catch and matched baseline trials, $t(47) = -0.124$, $p = .902$, Cohen's $dz = -0.018$, $BF_{01} = 6.331$; $t(47) = 1.075$, $p = .288$, Cohen's $dz = 0.155$, $BF_{01} = 3.708$ for the second and third trials respectively.



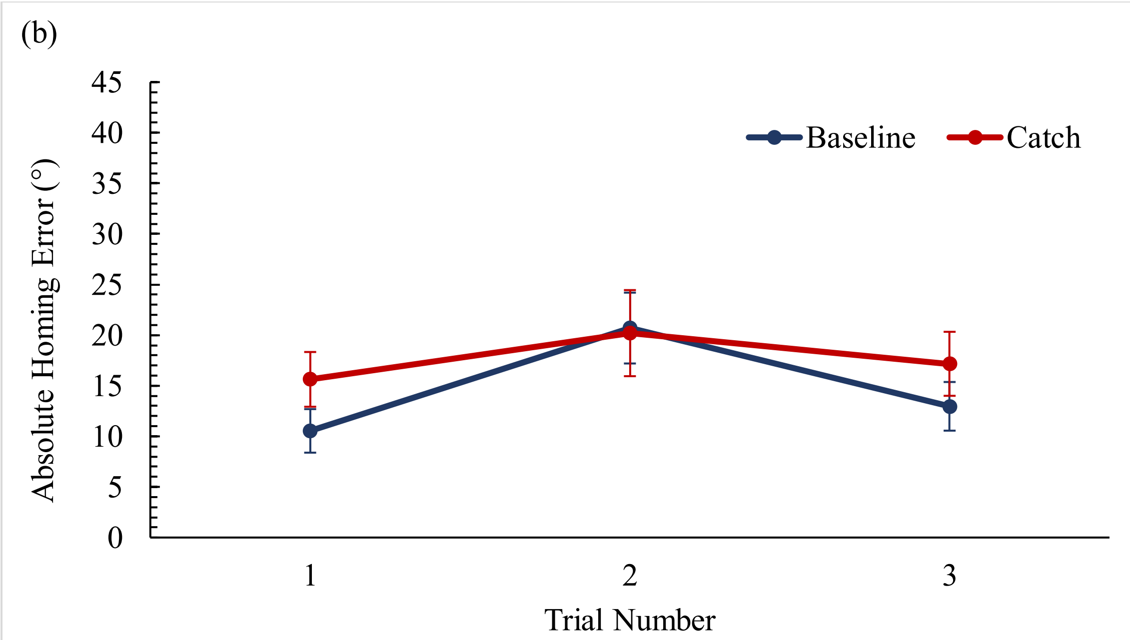


Figure 6. (a) Absolute homing error of each condition in Experiment 2. (b) Absolute homing error of the catch trials and the corresponding baseline trials as a function of trial number (1st to 3rd) in Experiment 2. The error bar was calculated by removing the error due to individual differences from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

4.3 Discussion

The results showed that comparable proportions of participants could identify the target ball on the first catch trial and on the first baseline trial. As participants could just have pointed to the ball that they thought to be the target, comparable recognition performance should have resulted in the comparable homing error. Consistently, the results showed that the homing errors were comparable on the first catch trial and the first baseline trial. Hence, the results of Experiment 2 supported the updating-spatial-views hypothesis over the suppression hypothesis.

However, the proportion of participants who recognized the target ball for the first catch and baseline trials (83.3% vs. 89.6%) was quite high. Although the rotation angle of 65° was carefully chosen to create 18% proportion difference according to the suppression hypothesis, one may still argue that the rotation angle of 65° was easy to detect and the null difference in Experiment 2 was attributed to ceiling effects. To address this issue, Experiment 3 was conducted with a reduced rotation angle to increase the recognition difficulty and replicate the null proportion difference between the first catch and baseline trials.

5. Experiment 3

Experiment 3 employed a rotation angle of 30° to increase the difficulty of recognizing the target ball. The updating-spatial-views hypothesis predicts no probability difference, whereas the suppressing hypothesis predicts a 14% difference between the first catch trial and the first baseline trial (as shown in Figure 4c). Additionally, participants were explicitly asked to choose the target ball before pointing to the home location during the homing phase of the catch and baseline trials.

5.1 Method

5.1.1 Participants

Forty-eight university students (24 females, 24 males) with normal or corrected-to-normal vision participated for credits in an introductory psychology course in Experiment 3.

5.1.2 Materials, design, and procedure

Experiment 3 was identical to Experiment 2 with the following exceptions. First, the distractor ball was rotated by 30°. Second, during the homing phase of both catch and baseline trials, participants were explicitly asked to indicate which ball (i.e., the right one or left one) they believed was located at the original location before pointing to it. The experimenter recorded the response by key pressing.

5.2 Results

5.2.1 Recognition performance

Table 2 shows the distribution of participants in different categories of recognition outcomes on the first catch and baseline trials. Among the 48 participants, 28 participants were correct for both the first catch and baseline trials (p_a=58.3%), 8 participants were correct for the first baseline trial but wrong for the first catch trial (p_b=16.7%), 8 participants were correct for the first catch trial but wrong for the first baseline trial (p_c=16.7%), and 4 participants were wrong for both the first catch and baseline trials (p_d=8.3%). The proportion of recognizing the target ball for the first catch trial ($p_a + p_c$) and for the first baseline trials ($p_a + p_b$) were both 75%, lower than those observed in Experiment 2.

McNemar's test did not show any significant difference in the proportion of participants who recognized the target ball for the first catch and baseline trials (75% vs. 75%), $X^2(1, N = 16) = 0.06$, $p = .803$. To qualify the null effect, we also calculated the Bayes Factor to compare the hypothesis of a null effect (i.e., $\frac{p_b}{p_b+p_c} = 0.5$) with the predicted effect of 14% (i.e., $\frac{p_b}{p_b+p_c} = 0.71$) [3]. The observed 8 participants in category B whereas 8 participants in category C, following a binomial distribution with a parameter ($\frac{p_b}{p_b+p_c}$) of 0.5 or 0.71, favored the null effect, $BF_{01} = 4.724$.

No proportion difference was founded for the second and third catch and baseline trials (see details in the supplementary materials).

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[3] Using the observed $p_b+p_c = 33.33\%$ and the predicted effect, $p_b - p_c = 14\%$, we get predicted $\frac{p_b}{p_b+p_c} = 0.71$ for the alternative hypothesis.

Table 2

Proportion of participants in different categories of recognition outcomes on the first catch trial and the first baseline trial in Experiment 3.

$p_a+p_b+p_c+p_d=1$		1st Catch Trial		
		Correct	Incorrect	
1st Baseline Trial	Correct	$p_a=\frac{28}{48}=58.3\%$	$p_b=\frac{8}{48}=16.7\%$	$p_a+p_b=75\%$
	Incorrect	$p_c=\frac{8}{48}=16.7\%$	$p_d=\frac{4}{48}=8.3\%$	
		$p_a+p_c=75\%$		

5.2.2 Homing Errors

Figure 7a illustrates the overall performance for each condition. The absolute homing error in the familiarity trials was not significantly different from the standard trials, $t(47) = 0.519$, $p = .606$, Cohen's $dz = 0.075$, $BF_{01} = 5.614$. The main effect of trial condition (all standard trials, catch trials, and baseline trials) was not significant, $F(2,94) = 1.015$, $p = .366$, $MSE = 33.947$, $\eta_p^2 = .021$.

Figure 7b illustrates the absolute homing error of each catch trial and the corresponding baseline trial. Homing error was comparable for the first catch trials and the first baseline trials, $t(47) = 0.924$, $p = .360$, Cohen's $dz = 0.133$, $BF_{01} = 4.267$. This result pattern was found for the following catch and matched baseline trials, $t(47) = 0.249$, $p = .804$, Cohen's $dz = 0.036$, $BF_{01} = 6.192$; $t(47) = 0.262$, $p = .795$, Cohen's $dz = 0.038$, $BF_{01} = 6.173$, for the second and third trials respectively.

In addition, participants had smaller absolute homing errors when they correctly recognize the target than when they did not (7° vs. 24°), $t(286) = -13.096$, $p < .001$, Cohen's $dz = -1.744$,

BF_{01} = 2.44e-28. This supports that participants used the correctly recognized target to indicate the home location.

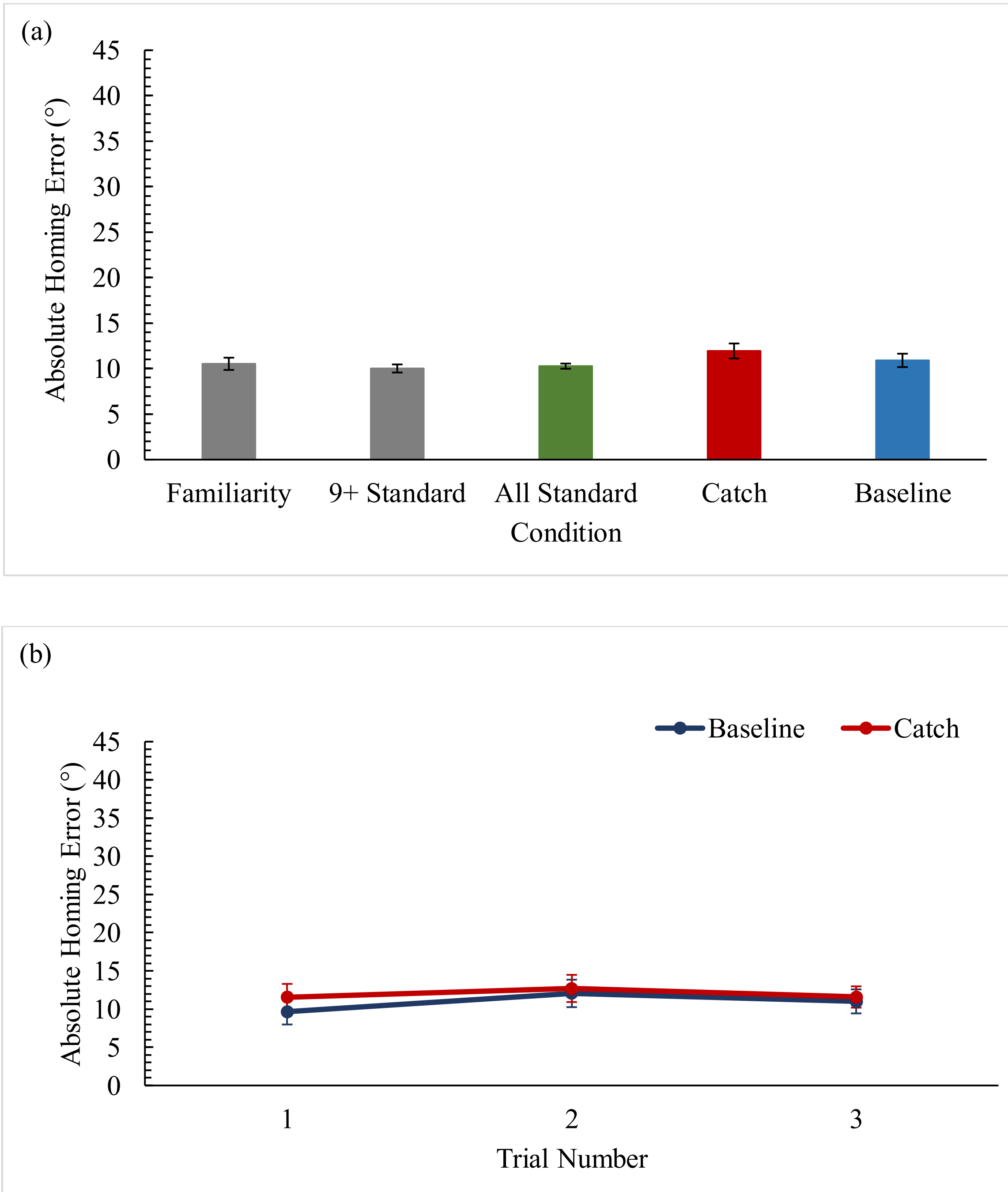

Figure 7. (a) Absolute homing error of each condition in Experiment 3. (b) Absolute homing error of the catch trials and the corresponding baseline trials as a function

of trial number (1st to 3rd) in Experiment 3. The error bar was calculated by removing the error due to individual variance from the standard error of each trial.

5.3 Discussion

Similar to Experiment 2, the results still showed that comparable proportions of participants could identify the target ball on the first catch trial and on the first baseline trial. In addition, the results showed that the homing errors were comparable on the first catch trial and the first baseline trial. Hence, the results of Experiment 3, replicating Experiment 2, also supported the updating-spatial-views hypothesis over the suppression hypothesis. As proportions of participants who could identify the target ball on the first catch trial and on the first baseline trial were 75%, the difficulty level of recognition should be intermedium (chance level is 50%). Thus, the null difference between the first catch and baseline trials should not be attributed to the ceiling or flooring effect.

While two balls were presented in both Experiments 2-3, Experiment 4 was conducted to extend the findings of Experiments 2-3 to recognizing two identical landmarks.

6. Experiment 4

The purpose of Experiment 4 was to further dissociate the updating-spatial-views hypothesis from the suppression hypothesis by testing whether participants could recognize ambiguous landmarks on the first catch trials. During the homing phase of the catch trials, two groups of landmarks were presented instead of two balls. In addition to the original group of the landmarks, we created a distractor group by randomly rotating the original group 65° clockwise or counterclockwise around the testing position. We also created new baseline trials to make them comparable to the catch trials. The new baseline trials were the same as the catch trials but preceded by another block of nine modified standard trials which always presented two copies of landmarks during the homing phase. Therefore, while participants expected to see the original landmarks during the homing phase of the first catch trial as in the previous experiments, they expected to see two copies of landmarks during the homing phase of the first baseline trial. The suppression hypothesis predicts that participants supressed path integration on the first catch trial but not on the first baseline trial. The proportion of participants who recognized the landmarks differed by 18% at a rotation angle of 65° (see Figure 4c). However, the updating-spatial-views hypothesis predicts that participants updated their views of the landmarks during the outbound path on the first catch trial, and these updated spatial views can remove the ambiguity of landmarks, resulting in no difference in the proportion of participants who recognized the landmarks between the first catch trial and the first baseline trial.

6.1 Method

6.1.1 Participants

Forty-eight university students (24 females, 24 males) with normal or corrected-to-normal vision participated for credits in an introductory psychology course.

6.1.2 Materials, Design, and Procedure

The materials, design, and procedure were the same as in Experiment 1b, with the following exceptions. First, during the homing phase of the catch trials, we presented two groups of landmarks (i.e., a group of original landmarks and a group of 65° rotated landmarks, see Figure 5b). Second, we added another block of 9 standard trials before the baseline trials. These standard trials were modified from the first 9 standard trials by presenting two groups of landmarks during the homing phase. Thus, while the first 9 standard trials (referred to as Standard trials #1) were used to create the expectation of seeing the original landmarks during the homing phase before the first catch trial, the 9 modified standard trials (referred to as Standard trials #2) were used to create the expectation of seeing two copies of landmarks during the homing phase before the baseline trials. Third, the baseline trials were identical to the catch trials. In particular, participants saw landmarks during the learning and outbound phases. In previous experiments, participants never saw landmarks for the baseline trials. However, as participants in Experiment 4 were asked to recognize the original landmarks on the baseline trials just as on the catch trials, such modification of baseline trials was necessary.

As a consequence, there were 33 trials in total in Experiment 4 in the order of the first nine standard trials #1 (familiarity trials), three catch trials mixed with another nine standard trials #1 (9+ standard trials #1), the nine standard trials #2, and the three baseline trials. The distractor group of landmarks were randomly rotated clockwise or counterclockwise from the original group of landmarks on all catch trials, the standard trials #2, and the baseline trials. Participants were asked to identify the original group of the landmarks (i.e., left or right group) verbally before they pointed to the original ball location (O). The experimenter recorded the response of the recognition task by key pressing.

6.2 Results

6.2.1 Recognition Performance

Table 3 shows the distribution of participants in different categories of recognition performance. Among the 48 participants, 31 participants were correct for both the first catch and baseline trials (p_a=64.6%), 7 participants were correct for the first baseline trial but wrong for the first catch trial (p_b=14.6%), 2 participants were correct for the first catch trial but wrong for the first baseline trial (p_c=4.2%), and 8 participants were wrong for both the first catch and baseline trials (p_d=16.7%).

McNemar's test did not show significant difference in the proportion of participants who recognized the target ball for the first catch and baseline trials (p_a+p_c=68.8% vs. p_a+p_b=79.2%), X^2 (1, N = 9) = 1.78, p = .182. To qualify the null effect, we also calculated the Bayes Factor to compare the hypothesis of a null effect (i.e., $\frac{p_b}{p_b+p_c} = 0.5$) with the predicted effect of 18% (i.e., $\frac{p_b}{p_b+p_c} = 0.979$)[4]. The observed 7 participants in category B whereas 2 participants in category C, following a binomial distribution of a parameter ($\frac{p_b}{p_b+p_c}$) of 0.5 or 0.979, favored the null effect, BF_{01} = 4.715.

No proportion difference was founded for the second and third catch and baseline trials (see details in the supplementary materials).

Table 3

Proportion of participants in different categories of recognition outcomes on the first catch trial and the first baseline trial in Experiment 4.

$p_a+p_b+p_c+p_d=1$		1st Catch Trial		
		Correct	Incorrect	
1st Baseline Trial	Correct	$p_a = \frac{31}{48}$ = 64.6%	$p_b = \frac{7}{48}$ = 14.6%	p_a+p_b= 79.2%
	Incorrect	$p_c = \frac{2}{48}$ = 4.2%	$p_d = \frac{8}{48}$ = 16.7%	
		p_a+p_c= 68.8%		

[4] Using the observed p_b+p_c = 18.8% and the predicted effect, p_b-p_c = 18%, we get predicted $\frac{p_b}{p_b+p_c} = 0.979$ for the alternative hypothesis.

6.2.2 Homing Errors

Figure 8a plots the overall performance for each trial condition. The absolute homing error in the familiarity trials was statistically significant from the 9+ standard trials #1, $t(47) = 2.204$, $p = .032$, Cohen's $dz = 0.318$, $BF_{01} = 0.707$. Thus, we only used 9+ standard trials #1 in the following test. The main effect of trial condition (the 9+ standard trials #1, the standard trials #2, the catch trials, and the baseline trials) was significant, $F(3, 141) = 12.448$, $p < .001$, $MSE = 4459.873$, $\eta_p^2 = .209$. The main effect was still significant after the Huynh-Feldt correction ($\varepsilon = 0.927$), $F(2.781, 130.716) = 12.199$, $p < .001$. Post-hoc testing using Bonferroni correction illustrated the following significant differences: the homing error was significantly larger in the catch trial condition, baseline trial condition and the standard trial #2 condition than in the 9+ standard trial #1 condition (mean difference = 11.306, $p < .001$, Cohen's $dz = 0.882$; mean difference = 10.858, $p < .001$, Cohen's $dz = 0.847$; mean difference = 11.207, $p < .001$, Cohen's $dz = 0.874$, respectively).

Figure 8b illustrates the absolute mean homing error cross all participants and the matched baseline trial. Homing error was not significantly different between the first catch trial and the first baseline trial, $t(47) = 0.979$, $p = .333$, Cohen's $dz = 0.141$, $BF_{01} = 4.063$. This pattern was also found for the second and third catch and matched baseline trials, $t(47) = 0.497$, $p = .622$, Cohen's $dz = 0.072$, $BF_{01} = 5.673$; $t(47) = -1.159$, $p = .252$, Cohen's $dz = -0.167$, $BF_{01} = 3.398$, for the second and third trials respectively.

In addition, participants had smaller absolute homing errors when they correctly recognize the original landmarks than when they did not (12° vs. 45°), $t\ (286) = -13.074$, $p < .001$, Cohen's *dz* = -1.763, BF_{01} = 2.95e-28. This supports that participants used the correctly recognized landmarks to indicate the home location.

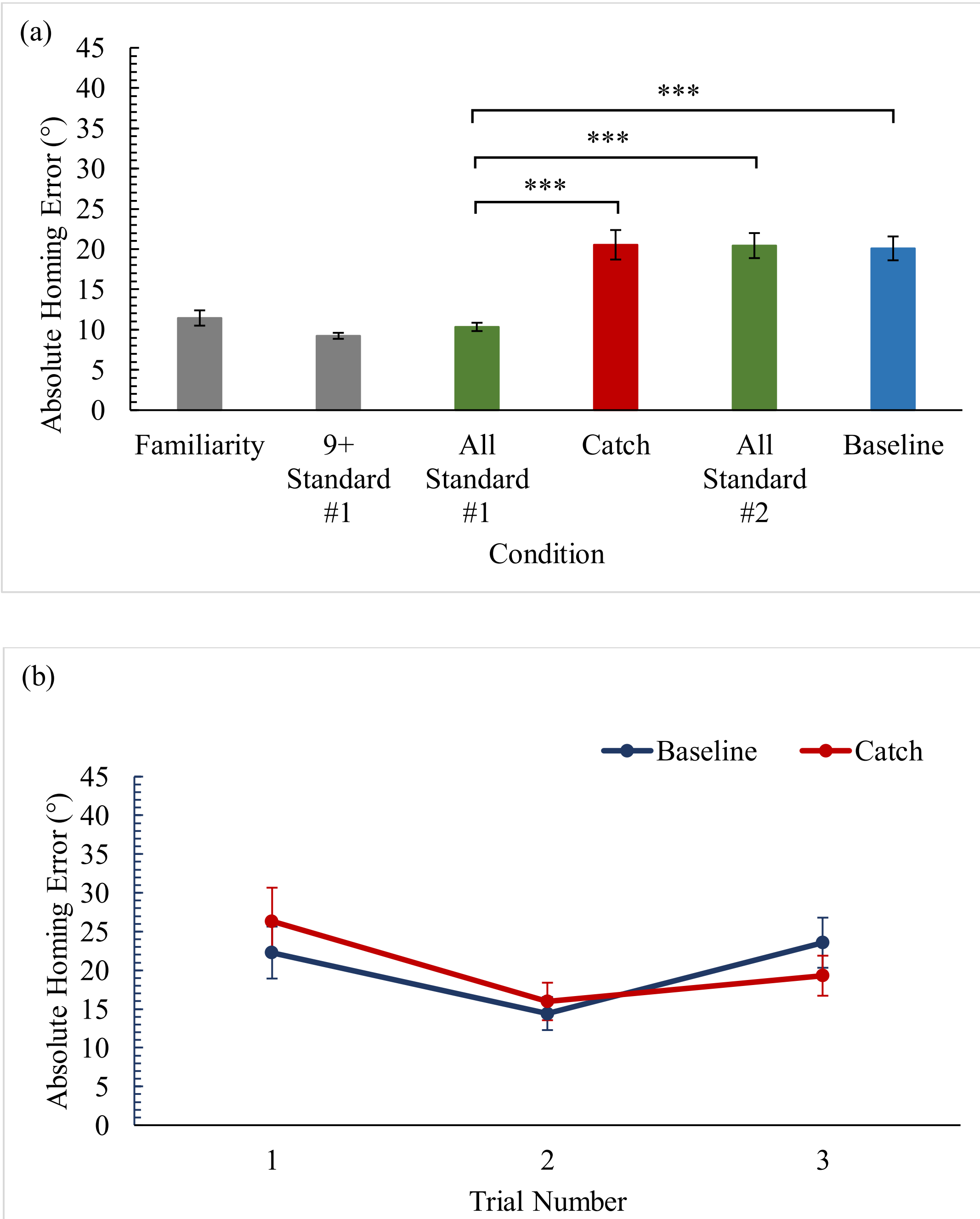

Figure 8. (a) Absolute homing error of each condition in Experiment 4. (b) Absolute homing error of the catch trials and the corresponding baseline trials as a function

of trial number (1st to 3rd) in Experiment 4. The error bar was calculated by removing the error due to individual variance from the standard error of each trial.

6.3 Discussion

The results showed that comparable proportions of participants were able to identify the original landmarks from distractor landmarks for the first catch trial and first baseline trial. Comparable proportions of participants who could identify the original landmarks from distractor landmarks should have resulted in the comparable homing errors, which was confirmed by the results of the null difference in homing errors for the first catch trial and first baseline trial. These results favored the updating-spatial-views hypothesis over the suppression hypothesis. Participants updated spatial views of the landmarks even on the first catch trial and used these updated spatial views of landmarks to recognize the original group of landmarks and then pointed to the home location based on the recognized group of landmarks.

7. General Discussion

The current study examined the role of path integration in a familiar environment with constantly available landmarks, yielding two important findings. First, it replicated Zhao and Warren's experiment 1 (2015b), by demonstrating that when no landmarks or targets were visually presented during the homing phase, homing angular error was significantly larger on the first catch trial than the first baseline trial. Second, when two targets or two groups of landmarks were presented during the homing phase, the proportion of participants who could use self-motion cues to recognize the original target or groups of landmarks was comparable on the first catch and baseline trials. Accordingly, homing angular error was comparable on the first catch and baseline trials. These findings support the updating-spatial-views hypothesis over the environment-independent hypothesis and the suppression hypothesis.

The key differences between the environment-independent hypothesis and the updating-spatial-views hypothesis lie in their assumption on the representations produced by path integration in a familiar environment with constantly available landmarks. The environment-independent hypothesis stipulates that irrespective of the environment's richness of landmarks, path integration produced independent spatial representations during locomotion. This hypothesis predicts that the independent representation from path integration should be available to guide homing when the landmarks are removed during homing. This hypothesis is consistent with the general belief that path integration is automatic and always active during locomotion, and that piloting is intermittent and resets path integration after locomotion (e.g., Etienne & Jeffery, 2004). This general belief has been supported by empirical findings (e.g., the Bayesian cue combination) using navigation in environments without constantly available landmarks (Chen et al., 2017; Shettleworth & Sutton, 2005; Zhang & Mou, 2017).

The updating-spatial-views hypothesis is consistent with the environment-independent hypothesis regarding independent spatial representations that are updated during locomotion in environments without constantly available landmarks. However, the updating-spatial-views hypothesis stipulates that in a familiar environment with constantly available landmarks, path integration is used to predict the spatial views of the environment during locomotion. The updated spatial views (imagery) are integrative representations consisting of both views and self-motion information (e.g., Tcheang et al., 2011). In this integrative representation, views are dominant over self-motion information (e.g., Du et al., 2020; Rieser, 1999). When real views are slightly different from the predicted views, real views can reset the errors in the path integration. For example, during navigation, participants predict that a familiar building is in the 90° clockwise direction relative to their body front, but they see the building actually in the 80° clockwise direction. They can correct the 10° error in estimating their heading and -10° error in estimating directions of other buildings (e.g., Wang, 2017).

However, when real views are totally different from the predicted views, the unexpected view mismatch might disrupt path integration. As an unexpected event captures attention (Horstmann, 2015), participants might not have the resources to maintain spatial representations in their working memory and then spatial representations updated from path integration might decay. Consequently, the view mismatch might disrupt the representations produced by path integration. For example, when participants predict that a familiar building in their 90° clockwise direction, but they do not see any building in the surrounding environment, the unexpected absence of the building might even disorient them. As a result, path integration might not be useful to guide homing when the landmarks are unexpectedly removed during homing.

Because the environment-independent hypothesis predicts independent spatial representations produced by path integration even in a familiar environment, it cannot explain the finding that homing angular error was significantly larger on the first catch trial than the first baseline trial in Experiments 1 and 1b of the current study as well as in experiment 1 of Zhao and Warren's study (2015b). In contrast, the updating-spatial-views hypothesis predicted that a totally unexpected mismatch between the predicted spatial views and the real view could disrupt spatial representations produced by path integration. Seeing repeated stable visual landmarks on every standard trial, participants might have formed a mental map of the stable environment and updated spatial views of the environment before the homing phase. However, during the homing phase of the first catch trial, out of their expectation, their real views of empty grassland did not match their predicted spatial views at all, which impaired spatial representations produced by path integration. As there was no landmark throughout the baseline trials, participants predicted the views of an empty grassland. Thus, no impairment should be expected on the baseline trials. Hence, the updating-spatial-views hypothesis can explain the larger homing angular error on the first catch trial than the first baseline trial in Experiments 1 and 1b of the current study as well as in experiment 1 of Zhao and Warren's study (2015b).

The key differences between the suppression hypothesis and the updating-spatial-views hypothesis lie in their assumptions on whether path integration is suppressed by the constantly available landmarks in a familiar environment. According to the suppression hypothesis, path integration is suppressed during locomotion, which is an appealing proposal for the following reasons. Visual landmarks always reset path integration (Mou & Zhang, 2014; Zhao & Warren, 2015a). Thus, spatial estimates from path integration seem useless when landmarks are always available. If path integration consumes cognitive resources (Amorim et al., 1997; He & McNamara, 2018; Lu et al., 2020), it is wise to suppress useless path integration when landmarks are always available. More specifically, this hypothesis predicts that when landmarks are always available, path integration is suppressed and cannot be used to guide either homing or recognition.

By contrast, according to the updating-spatial-views hypothesis, path integration is not suppressed during locomotion in a familiar environment with constantly available landmarks. Rather, path integration is used to update the spatial views (imagery) of the familiar environment during locomotion. This hypothesis argues that although visual landmarks always reset path integration, path integration is not necessarily useless when visual landmarks always are available. The predicted views updated by the path integration can facilitate scene recognition (e.g., Wang & Simons, 1999) and remove spatial ambiguity created by identical landmarks (e.g., Sharp et al., 1990). As discussed above, a mismatch between the real view of the empty grassland and the predicted spatial view of visual items in the environment might disorient participants. However, a real view of two groups of landmarks or two targets are partially overlapped with the predicted spatial view, so no disorientation occurs. People can use the updated spatial views to recognize the correct target and correct landmarks. More specifically, this hypothesis predicts that path integration in a familiar environment with constantly available landmarks is useful for recognition although it may not be useful for homing.

Therefore, both the suppression hypothesis and the updating-spatial-views hypothesis can explain the finding that homing angular error was significantly larger on the first catch trial than the first baseline trial in Experiments 1 and 1b of the current study as well as in experiment 1 of Zhao and Warren's study (2015b). However, only the updating-spatial-views hypothesis can explain the finding of no impairment in recognizing the landmarks or targets on the first catch trial compared with the first baseline trial in Experiments 2-4 in the current study.

The finding of no impairment in recognition on the first catch trial in Experiments 2-4 should not be attributed to a ceiling or floor effect in recognition. Following Figure 4c (which assumed that path integration was suppressed), we can see that when the rotation angle of the distractor target or landmarks is too large, recognition performance was perfect even on the first catch trial, indicating a ceiling effect. When the rotation angle of the distractor is too small, recognition performance was at the chance level (50%) even on the first baseline trial, indicating a floor effect. However, we carefully chose the rotation angle to avoid the ceiling or floor effect. In particular, we used a rotation angle of 65° in Experiments 2 and 4, and 30° in Experiment 3. According to Figure 4c, the probability of recognizing the correct target or landmarks should be 18% lower for a rotation angle of 65° and 14% lower for a rotation angle of 30° on the first catch trial than for the first baseline trial. Moreover, the results showed that the overall recognition accuracy in Experiments 3 and 4 was around 75%, indicating an intermediate level of difficulty in recognition.

The lack of impairment in recognition on the first catch trial in Experiments 2-4 should not be attributed to a false negative (type II error) either. We recruited 48 participants, which can detect a significant proportion difference in successful recognition between the first catch and baseline trials with a probability larger than 91% (as shown in the power analysis in Experiment 2). Moreover, all null effects on recognition performance of Experiments 2-4 were supported by Bayes Factors (BF_{01}s $\geq$ 4.715). Additionally, no impairment in recognition should result in no impairment in homing, indicated by the lack of effect on homing errors and the corresponding Bayes Factors (BF_{01}s $\geq$ 3.123).

The updated spatial views proposed in the updating-spatial-views hypothesis are an integrative representation consisting of both spatial views (imagery) and self-motion information (e.g., what I will see if I turn right 90°). A similar integrative representation consisting of visual representations and motion-related representations has been proposed in the literate (e.g., the coupling between representation and action in Rieser, 1999; the multimodal representation in Tcheang et al., 2011). In addition, studies on neural bases of human navigation have shown the cue-independent (i.e., integrative) spatial representations for landmarks and self-motion cues in human retrosplenial cortex (e.g., Chen et al., 2022). However, no previous studies have showed that an integrative representation during locomotion could result in impaired homing estimates based on self-motion cue alone. Some studies have even suggested the opposite (Kalia, Schrater, & Legge, 2013; Philbeck & O'Leary, 2005; Rieser, 1999). Participants who have already created a mental image of the environment in their mind will recall the location of a target more accurately without vision (Rieser, 1999). So how can an integrative representation during locomotion cause impaired homing performance on the first catch trial reported in experiment 1 of Zhao and Warren's study (2015b)? The updating-spatial-views hypothesis extends the proposal of the integrative representation by suggesting that an unexpected real view of empty grassland after locomotion might result in disorientation. This extended proposal can solve the puzzle of how an integrative representation updated during locomotion could cause impaired performance in homing on the first trial reported by Zhao and Warren's study (2015b).

While the updating-spatial-views hypothesis clearly emphasizes the importance of matching real views with updated spatial views during homing, it remains unclear whether such a match occurs during locomotion as well. Previous studies have shown that displaced visual landmarks presented during homing can reset participants' orientation and position, whereas those presented during the outbound path are ignored (Mou & Zhang, 2014; Zhang & Mou, 2017). In a familiar environment with constantly available landmarks, people can potentially compare predicted views with real views as often as they like. However, frequent view comparison might be cognitively expensive and may not be an efficient way for navigation. Therefore, it may be the case that people only compare the predicted views updated by path integration with the real views after locomotion or when they are explicitly instructed to do so. Future study is needed to investigate the stages at which view comparison occurs in a familiar environment with constantly available landmarks.

The updating-spatial-views hypothesis suggests that spatial representations updated by path integration were impaired by the unexpected removal of landmarks on the first catch trial in Experiments 1 and 1b. However, it is not clear whether the unexpected removal of the landmarks impaired participants' heading estimates, position estimates, or both. If the unexpected removal of landmarks only impairs one estimate (e.g., impaired heading) but does not impair the other (e.g., intact position), it would provide further evidence that path integration is used to update both the position and heading of participants during the outbound path, but one estimate is impaired by a view mismatch during homing. Future studies that separately measure heading errors, position errors, and homing errors (Mou & Zhang, 2014) should be conducted to this possibility.

In conclusion, the current study provides evidence that path integration based on self-motion cues is not suppressed in a familiar environment with constantly available landmarks. Rather, this process updates spatial views of the environment, which can help facilitate scene recognition and reduce spatial ambiguity to aid landmark-based navigation. Nevertheless, unexpected failure to see predicted views may disrupt spatial representations from path integration. These findings have implications for our understanding of how both self-motion cues and landmark information jointly contributes to spatial navigation in a familiar environment.

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Supplementary

Table S1

The trial order in Experiment 1

<table>
<tr><td></td><td>Standard trials/ familiarity trials (9 trials)</td><td rowspan="4">→</td><td>Standard trials (9 trials)</td><td rowspan="4">Mixed with</td><td>Catch trials (3 trials)</td><td rowspan="4">→</td><td>Baseline trials (3 trials)</td></tr>
<tr><td>Learning phase</td><td rowspan="3">Stable visual cues</td><td rowspan="3">Stable visual cues</td><td rowspan="2">Stable visual cues</td><td rowspan="3">No visual cues</td></tr>
<tr><td>Outbound phase</td></tr>
<tr><td>Homing phase</td><td>No visual cues</td></tr>
</table>

Table S2

Proportion of participants in different categories of recognition performance for the second and third catch trials and baseline trials in Experiment 2.

$p_a+p_b+p_c+p_d=1$		2nd Catch Trial		
		Correct	Incorrect	
2nd Baseline Trial	Correct	$p_a=\frac{30}{48}=62.5\%$	$p_b=\frac{5}{48}=10.4\%$	$p_a+p_b=72.9\%$
	Incorrect	$p_c=\frac{7}{48}=14.6\%$	$p_d=\frac{6}{48}=12.5\%$	
		$p_a+p_c=77.1\%$		

$p_a+p_b+p_c+p_d=1$		3rd Catch Trial		
		Correct	Incorrect	
3rd Baseline Trial	Correct	$p_a=\frac{35}{48}=72.9\%$	$p_b=\frac{8}{48}=16.7\%$	$p_a+p_b=89.6\%$
	Incorrect	$p_c=\frac{4}{48}=8.3\%$	$p_d=\frac{1}{48}=2.1\%$	
		$p_a+p_c=81.2\%$		

Table S3

Proportion of participants in different categories of recognition performance for the second and third catch trials and baseline trials in Experiment 3.

$p_a+p_b+p_c+p_d=1$		2nd Catch Trial		
		Correct	Incorrect	
2nd Baseline Trial	Correct	$p_a=\frac{28}{48}=58.3\%$	$p_b=\frac{5}{48}=10.4\%$	$p_a+p_b=68.75\%$
	Incorrect	$p_c=\frac{8}{48}=16.7\%$	$p_d=\frac{7}{48}=14.6\%$	
		$p_a+p_c=75.0\%$		

$p_a+p_b+p_c+p_d=1$		3rd Catch Trial		
		Correct	Incorrect	
3rd Baseline Trial	Correct	$p_a=\frac{26}{48}=54.2\%$	$p_b=\frac{12}{48}=25\%$	$p_a+p_b=79.2\%$
	Incorrect	$p_c=\frac{6}{48}=12.5\%$	$p_d=\frac{4}{48}=8.3\%$	
		$p_a+p_c=66.7\%$		

Table S4

Proportion of participants in different categories of recognition performance for the second and third catch trials and baseline trials in Experiment 4.

$p_a+p_b+p_c+p_d=1$		2nd Catch Trial		
		Correct	Incorrect	
2nd Baseline Trial	Correct	$p_a=\frac{30}{48}=62.5\%$	$p_b=\frac{6}{48}=12.5\%$	$p_a+p_b=75\%$
	Incorrect	$p_c=\frac{8}{48}=16.7\%$	$p_d=\frac{4}{48}=8.3\%$	
		$p_a+p_c=79.2\%$		

$p_a+p_b+p_c+p_d=1$		3rd Catch Trial		
		Correct	Incorrect	
3rd Baseline Trial	Correct	$p_a=\frac{28}{48}=58.3\%$	$p_b=\frac{2}{48}=4.2\%$	$p_a+p_b=62.5\%$
	Incorrect	$p_c=\frac{9}{48}=18.8\%$	$p_d=\frac{9}{48}=18.8\%$	
		$p_a+p_c=77.1\%$		