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Piloting Systems Reset Path Integration Systems During Position Estimation

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During locomotion, individuals can determine their positions with either idiothetic cues from movement (path integration systems) or visual landmarks (piloting systems). This project investigated how these 2 systems interact in determining humans' positions. In 2 experiments, participants studied the locations of 5 target objects and 1 single landmark. They walked a path after the targets and the landmark had been removed and then replaced the targets at the end of the path. Participants' position estimations were calculated based on the replaced targets' locations (Mou & Zhang, 2014). In Experiment 1, participants walked a 2-leg path. The landmark reappeared in a different location during or after walking the second leg. The results showed that participants' position estimations followed idiothetic cues in the former case, but the displaced landmark in the latter case. In Experiment 2, participants saw the displaced landmark when they reached the end of the second leg and then walked a third leg without the view of the landmark. Participants were asked or not to point to 1 of the targets before they walked the third leg. The results showed that the initial position of the third leg was still influenced by the displaced landmark in the former case, but was determined by idiothetic cues in the latter case. These results suggest that the path integration system works dynamically and the piloting system resets the path integration system when people judge their positions in the presence of conflicting piloting cues.

Keywords: position estimation, heading estimation, path integration, piloting system, landmark

Determining one's position during navigation is considered one of the most primitive cognitive abilities of humans and most mobile animals (Etienne & Jeffery, 2004; Klatzky, Loomis, Beall, Chance, & Golledge, 1998; Souman, Frissen, Sreenivasa, & Ernst, 2009; Wehner, 2003). To study how humans and any mobile animals determine their positions, researchers have distinguished two different navigation systems: the path integration system and the piloting system (Gallistel, 1990; Gallistel & Matzel, 2013). The aim of this project was to investigate how these two systems interact in determining humans' positions.

The path integration system uses cues generated by self-movement to get one's moving direction and speed, and then calculates one's position relative to some point on the traversed path (i.e., the origin of the path). These cues include vestibular cues, proprioceptive cues, motor efference copies, and optical flow (Etienne & Jeffery, 2004; Klatzky et al., 1998; Loomis et al., 1993; Tcheang, Bülthoff, & Burgess, 2011; Warren, Kay, Zosh, Duchon, & Sahuc, 2001). All of these cues are referred to as *idiothetic cues* (Whishaw & Brooks, 1999). All of them, with the exception of optical flow, are also referred to as *inertial cues* (Tcheang et al., 2011). Some studies suggest that the path integration system only maintains the homing vector (i.e., the vector from the current position to the origin) and does not represent the path's configuration. Hence, path integration is a continuous updating process in which navigators need to represent the homing vector, add it to the vector of a new movement, and therefore obtain the new homing vector (Etienne & Jeffery, 2004; Shettleworth & Sutton, 2005; Wiener, Berthoz, & Wolbers, 2011). Other studies indicate that the path integration system might represent the path configuration (Fujita, Klatzky, Loomis, & Golledge, 1993). Using the configural knowledge of the path, navigators can calculate vectors between any two points on the route that has been traversed. A recent study showed that, depending on their intention, humans might have the capacity to encode either the homing vector or the path configuration (Wiener et al., 2011). In the current project, we assume that humans' path integration system can represent vectors from the current location to multiple other locations in an environment, including the origin of the path (Loomis et al., 1993; Loomis, Klatzky, Golledge, & Philbeck, 1999; Rieser, Hill, Talor, Bradfield, & Rosen, 1992; Wang & Brockmole, 2003).

Piloting is the other way of determining one's position during navigation. When navigators come to a new environment, they learn the spatial relationships between some visual items (e.g., landmarks) and themselves. Navigators' positions are specified with respect to the distance and bearing relative to the visual items. These specifications are kept in navigators' memory (Cheng & Spetch, 1998). Navigators then can use the specifications in memory to determine their positions whenever they see the visual items in this environment independent of the path integration system. The role of such landmarks in navigation has been explored for a long time in literature. Many studies have indicated its importance,

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particularly when navigators need to travel over a long distance and the path integration system is not reliable (e.g., Dyer, 1991; Etienne, Maurer, Boulens, Levy, & Rowe, 2004).

The path integration system and the piloting system can work independently (Chen & McNamara, 2014; Doeller & Burgess, 2008; Etienne & Jeffery, 2004; Etienne et al., 2004; Klatzky et al., 1998; Nardini, Jones, Bedford, & Braddick, 2008; Wiener et al., 2011; Zhao & Warren, 2015a, 2015b). On one hand, people can navigate effectively by relying only on their path integration system. For example, in a study by Klatzky et al. (1998), blindfolded participants walked a 2-leg path, and then, from the end of the path, they were asked to point to its origin. The results showed that participants performed this task accurately. As participants required vision to use the piloting system, their accuracy in pointing to the origin of the path could only be attributed to the path integration system. On the other hand, people can also navigate by relying strictly on the piloting system. For example, Nardini et al. (2008) demonstrated that human adults and children could locate a target relative to other objects after disorientation. Because the path integration system was disrupted during disorientation, the successful localization of the target could only be attributed to the piloting system.

In everyday life navigation, however, both visual landmarks and idiothetic cues are usually available. The interaction between the path integration system and the piloting system in human navigation is critical but has not been well examined (Mou & Wang, 2015). To investigate how these two systems interact, we tested three competing hypotheses in the current study. Before we describe the hypotheses, we first review relevant theories and empirical works on which the hypotheses were based.

There are two key claims to the prevailing theory on the interaction between these two systems. First, the path integration system dynamically (continuously) updates one's position, and the piloting system intermittently (not continuously) corrects the error accumulated in the path integration system (Etienne et al., 2004; Gallistel, 1990; Goodridge & Taube, 1995; Müller & Wehner, 1988; Taube & Burton, 1995; Valerio & Taube, 2012). Second, once the piloting system corrects the errors of the estimated position in the path integration system, the path integration system uses the corrected position as the initial position of the next new movement (Etienne et al., 2004). According to this theory, the path integration system functions "online," and it requires that the distance and direction of every new movement are added to the homing vector to calculate the new homing vector; the piloting system is an offline system relying on the long-term memory of landmarks (Cheng & Spetch, 1998). Because of the possible noise in estimating the distance and direction of every new movement, the errors in estimating the homing vector are accumulated along a path in the path integration system. In contrast, the estimation errors in the piloting system do not accumulate along the path because this system relies on the long-term memory (Etienne et al., 2004). Hence, the piloting system can reset and remove errors accumulated in the path integration system.

In the prevailing theory, the first claim is that the piloting system intermittently reset the path integration system. That claim is primarily supported by animal studies showing that displaced landmarks determine animals' homing behaviors (Collett & Collett, 2000; Etienne et al., 2004; Shettleworth & Sutton, 2005) and the firing fields of rodents' place cells (Knierim, Kudrimoti, & McNaughton, 1998; Yoder, Clark, & Taube, 2011). This proposal might also be valid in human heading estimations. A few human studies showed that displaced distal landmarks overrode the heading indicated by the path integration system (Mou & Zhang, 2014; Zhao & Warren, 2015a, 2015b). However, it is not clear whether and when the piloting system resets the path integration system in humans' position estimations.

In a human study, Tcheang et al. (2011) challenged the prevailing theory by questioning whether the piloting system intermittently reset the path integration system in humans' position estimations. They instead proposed that humans determine their positions using both idiothetic cues and visual cues continuously, and thus form a coherent multimodal representation of the traversed path. Tcheang et al. manipulated the rotation and translation gains of the visual projection to make the visual input inconsistent with the motion-related cues in an immersive virtual environment (e.g., participants physically rotated 130°, but the visual input indicated a rotation of 90°). After the adaption phase, participants walked an outbound path and then back to the origin of the path in darkness. The results showed that the homing behavior was affected by the adapted gain. Tcheang et al. argued that instead of using inertial cues dynamically and visual cues intermittently, humans use both visual cues and inertial cues dynamically to update their positions and then develop an enduring multimodal representation of the traversed path.

The second key claim of the prevailing theory speculates that after the piloting system corrects the errors of the estimated position in the path integration system, the path integration system uses the corrected position as the initial position of the next new movement (Etienne et al., 2004). Etienne et al. (2004) tested this claim on hamsters. In their study, hamsters lived in a circular arena with several patterned walls outside of the arena. Before the hamsters left their nest, the circular arena was rotated by 135°. The hamsters walked to one location in darkness. Then the environment was lit up for 10 to 12 s so that they could view the patterned walls. The hamsters walked another leg in darkness, and they then found their way home by themselves in darkness. The results showed that hamsters relied on the visual landmarks to find their way home, suggesting that the piloting system, which was available when the environment was lit up, overrode the position estimated by the path integration system. More critically, when the light was turned off again, the path integration system used the overridden position as the initial position of the new movement.

Does humans' path integration system use the corrected position as the initial position of a new movement? There are no human studies that can directly answer this question. The cue combination studies in human spatial cognition, however, seem to imply that the answer is "no" (see Cheng, Shettleworth, Huttenlocher, & Rieser, 2007, for a review; see also Chen & McNamara, 2014; Nardini et al., 2008; Zhao & Warren, 2015a). In a typical cue combination study, after learning the locations of three objects, adult participants walked a 2-leg path in the presence of three landmarks. Then, in the testing phase, they needed to locate the objects using (a) landmark cues only, (b) the path integration system only, (c) consistent cues from both systems (cues from the two systems indicating that the objects were in the same locations), or (d) conflict cues from both systems (cues from the two systems indicating that the objects were in different locations). The results showed that human adult participants in the "both cues" conditions combined these two cues in a weighted average, and the weight was negatively correlated with the variance of the estimated locations in the single cue conditions.

The key assumption in the cue combination studies is that spatial information (e.g., a target's location) specified by either cue is encoded separately. Although the representations of separate cues can be combined during tests to better estimate a target location, the separate spatial representation determined by either separate cue is not modified or replaced by the weighted estimation.[1] In line with this idea, the path integration system and the piloting system might separately determine people's positions. Although people can combine these two systems to determine their positions, these two separate position representations do not modify each other. Therefore, during a new movement in which the piloting cue is no longer available, contrary to the claim of the prevailing theory, humans' path integration system might use the estimated position in its own system, but not the corrected one provided by the piloting system, as the initial position of a new movement.

In the current study, we proposed and tested three hypotheses on how the piloting and the path integration systems are interactively used to estimate humans' positions. The first hypothesis elaborates upon the prevailing theory. It claims that the path integration system dynamically updates one's position and the piloting system intermittently resets the path integration system; this hypothesis also claims that the path integration system uses the position corrected by the piloting system as the initial position of a new movement. In this hypothesis, we further propose that the resetting process occurs when people need to judge their positions in an environment. When people judge their positions, they retrieve the separate position representations produced by the path integration system and by the piloting system. If the discrepancy between the two estimated positions is significant, resetting occurs. We refer to this hypothesis as the *retrieval-invoked resetting hypothesis*.

The second hypothesis contrasts the retrieval-invoked resetting hypothesis by stipulating that resetting occurs whenever conflicting inertial cues and visual cues are available. This hypothesis is consistent with the proposal that people use both visual cues and inertial cues to dynamically update their positions (Tcheang et al., 2011). We note that Tcheang et al. (2011) did not explicitly state that visual cues reset idiothetic cues continuously, although they stipulated that people use visual cues as well as idiothetic cues to determine their positions continuously. We refer to our second hypothesis as the *continuous resetting hypothesis.*

The third hypothesis differs from the retrieval-invoked resetting hypothesis by claiming that although visual cues could override the estimated position in the path integration system, the path integration system uses its own position representation as the initial position of any new movement when visual cues are removed. This hypothesis is consistent with the key assumption of the cue combination models that the weighted position representation does not change the separate position representations in the path integration system and in the piloting system. We refer to this hypothesis as the *combination without resetting hypothesis*.

Two experiments were designed to test these three hypotheses. Experiment 1 was designed to differentiate the retrieval-invoked resetting hypothesis from the continuous resetting hypothesis. In particular, one displaced landmark was presented when participants were required or not to determine their positions. The retrieval-invoked resetting hypothesis predicted that participants who were required to determine their positions in the presence of the landmark would use the displaced landmark to override idiothetic cues in humans' position estimations, whereas participants who were not required to do so would ignore the displaced landmark. In contrast, the continuous resetting hypothesis predicted that participants would use the displaced landmark to override their positions estimated by idiothetic cues regardless of whether or not they were required to determine their positions in the presence of the displaced landmark.

Experiment 2 was designed to differentiate the retrieval-invoked resetting hypothesis from the combination without resetting hypothesis and the continuous resetting hypothesis in a single experiment. Similar to Experiment 1, one displaced landmark was presented when participants were required or not to determine their positions. Furthermore, after the presence of the displaced landmark, participants walked a new leg. The retrieval-invoked resetting hypothesis predicted that participants who were required to determine their positions in the presence of the landmark would use the position corrected by the landmark as the initial position of the new leg. However, such resetting would not occur for participants who were not required to determine their positions in the presence of the landmark. The continuous resetting hypothesis predicted that resetting would occur regardless of whether or not participants were required to determine their positions in the presence of the displaced landmark. According to the combination without resetting hypothesis, the path integration system uses the position representation in its own system as the start of the new leg when the piloting cue is no longer available during the new leg. Therefore, no resetting would be observed when participants walked the new leg regardless of whether or not participants needed to determine their positions in the presence of the displaced landmark.

Before describing the experiments in details, it is important to review the method used to calculate participants' position estimations. We calculated these estimations after participants walked a path using the method developed in our recent study (Mou & Zhang, 2014). In it, we proposed that a participant's estimated position and heading after walking a path can be calculated if the participant points to the origin of the path and another location. As shown in Figure 1, the participant initially learns the location of the origin, O, and another object, X. Then they travel from O to T and from T to P. While standing in P and facing H, the participant is asked to point to the location of O and X. Suppose they actually point to O′ and X′ as the estimations of O and X, respectively. We proved mathematically that the estimated position (P′) and heading (H′) could be calculated according to the following two equations (Mou & Zhang, 2014; we have also included one modified version of the proof in the Appendix):

$$\mathrm{OP}' = \alpha - \alpha' + \mathrm{OP};$$
$$\mathrm{H}' = \alpha - \alpha' - \beta + \mathrm{H}.$$

[1] Researchers may have different interpretations of the combination theories regarding whether or not the separate spatial representation determined by either cue is modified or replaced by the weighted estimation. In the current project, we take the strictest interpretation that the separate spatial representations are combined, but not changed, during spatial judgments. Therefore, the current study tested this specific interpretation rather than all interpretations of the combination theories.

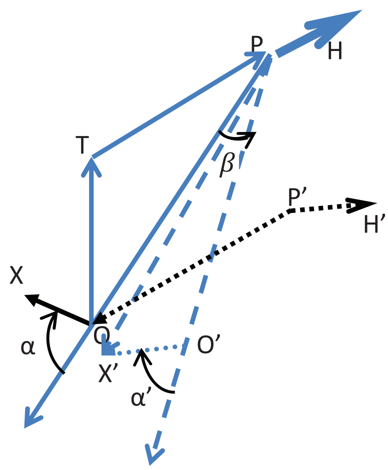

Figure 1. Dissociate the heading estimation and the position estimation using the errors in pointing to the origin (O) and one object (X). A hypothetical participant walks a path, starting from O (origin) and ending at P (testing position). The turning point is T. The participant's testing heading is referred to as H. The estimated position of O is O′, and of X is X′. The estimated testing position is P′ and the estimated testing heading is H′. Beta (β) is the signed angular distance from the direction of PO to the direction PO′. Alpha (α) is the signed angular distance from the direction of PO to the direction of OX. Alpha prime (α′) is the signed angular distance from the direction of PO′ to the direction of O′X′. Clockwise angular distances are positive. See the online article for the color version of this figure.

In these equations, OP′ is the allocentric bearing from O to P′, whereas OP is the allocentric bearing from O to P. H and H′ are the allocentric headings. In the current article, we use the definitions of bearings and headings in Klatzky (1998). According to Klatzky, a bearing specifies the direction between two points with respect to a reference direction, whereas a heading specifies the orientation of an object (including a person) with respect to a reference direction. Mathematically, a reference direction can be any direction in the horizontal plane. In the current study, as we do not aim to investigate how people select a reference direction, for simplicity, we use the direction from O to T (the first walking direction) as the reference direction. The bearings OP′, OP, H, and H′ are all specified as signed angular distances with respect to the bearing of OT. The bearing of OT is 0°. A clockwise angular distance is positive. Alpha (α) is the signed angular distance from the bearing of PO to the bearing of OX; α′ is the signed angular distance from the bearing of PO′ to the bearing of O′X′; and β is the signed angular distance from the bearing of PO to the bearing of PO′. Again, all the bearings of PO, OX, PO′, and O′X′ are specified as signed angular distances from the bearing of OT. In the interest of simplicity, in the following texts, we use two letters to indicate a bearing. In particular, AB indicates the bearing from A to B.

As previous studies have indicated that individuals tend to underestimate the distance in a virtual environment (Thompson et al., 2004), we only use the direction of OP′, instead of both the direction and the length of OP′, as the position estimation.

Experiment 1

The purpose of this experiment was to differentiate between the retrieval-invoked resetting hypothesis and the continuous resetting hypothesis in terms of humans' position estimations. In this experiment, participants studied the locations of five targets in addition to a single landmark.[2] One target was placed at the origin, O (see Figure 2). A target was the probe, of which participants would estimate the position during testing, whereas the landmark was a visual cue indicating a location in the environment. After learning the object array and the landmark, participants walked a 2-leg path (O-T and T-P in Figure 2) after the targets had been removed. At the end of the traversed path, standing at P and facing H, they used a stick to replace the five targets. Where the target was placed was defined as the response location. The participants' estimated testing positions (OP′) and headings (H′) were calculated based on the response locations (Mou & Zhang, 2014). The landmark disappeared when participants started to walk the path. The key manipulation was as follows: In one condition, the displaced landmark reappeared when participants started to walk the second leg and disappeared again when participants reached the end of the second leg (*conflictATwalking* condition); in the other condition, the displaced landmark reappeared when participants reached the end of the second leg and while they replaced targets in the test phase (*conflictAFTERwalking* condition). In both conditions, the displaced landmark reappeared at the testing position (P), indicating a conflicting position.

The continuous resetting hypothesis and the retrieval-invoked resetting hypothesis have different predictions about when the displaced landmark determined participants' estimations of their testing positions (see Table 1). The continuous resetting hypothesis stipulates that people continuously use the piloting system to estimate their positions. Thus, the resetting process would occur in both the conflictATwalking and conflictAFTERwalking conditions. In other words, the displaced landmark would determine participants' estimated positions in both conditions. By contrast, the retrieval-invoked resetting hypothesis stipulates that people intermittently use the piloting system to reset the path integration system. When people judge their positions in an environment in the presence of the conflicting piloting cues, the resetting occurs. Thus, the displaced landmark would affect the position estimation only in the conflictAFTERwalking condition, in which the displaced landmark was presented during the judgments of the targets' locations, but not in the conflictATwalking condition, in which the displaced landmark was presented when participants were not required to make judgments. We also included the third condition (*consistent* condition), in which the landmark reappeared at the same location, to obtain the baseline position estimation when the landmark and idiotheic cues indicated the same testing position. The cues determining the estimation of the testing position according to these two hypotheses are listed in Table 1.

[2] In the current project, a landmark refers to any visual item that can indicate a location in an environment (e.g., Doeller & Burgess, 2008; Nardini et al., 2008). This is different from a stable and large item used as a landmark in an environment (e.g., Gallistel, 1990).

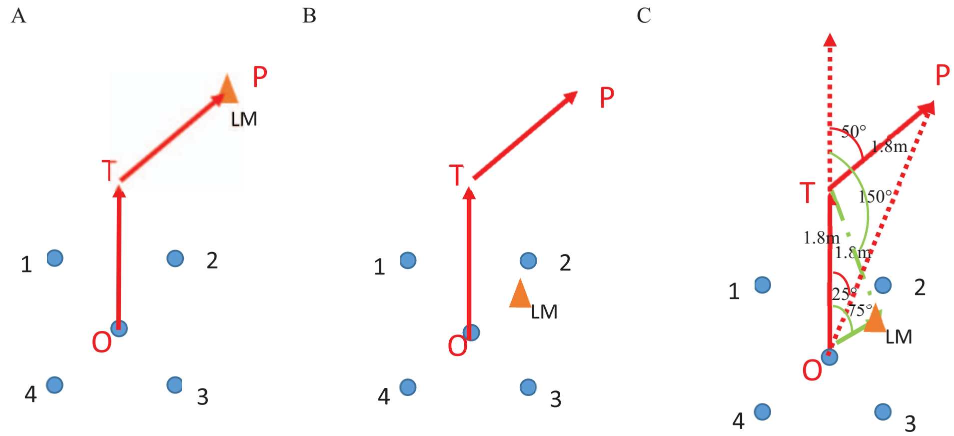

Figure 2. Schematic diagram of the experimental setup in Experiment 1. The 2-leg path has the origin (O), the turning point (T), and the ending position (P). All the targets, the landmark, and the path are presented together only for readers. Five dots are denoted as five targets (one is placed at the origin, and the other four are numbered as 1–4). The triangle is denoted as the landmark (LM). Panel A: In the consistent condition, the landmark was placed at the end of the path. Panel B: In the conflictATwalking and the conflictAFTERwalking conditions, the landmark was originally placed at one other location. Panel C: Measures in the conflictATwalking and conflictAFTERwalking conditions. Lengths of vectors: OT = TP = T-LM = 1.8 m. Directions of vectors with respect to OT: TP = 50°, T-LM = 150°, O-LM = 75°, OP = 25°. See the online article for the color version of this figure.

Method

Participants. Thirty-six university students (18 men and 18 women) participated in the experiment to fulfill the partial requirement for an introductory psychology course.

Materials and design. The physical experimental room was a 4 m × 4 m square room. The virtual environment was displayed in stereo with an nVisor SX60 head-mounted display (HMD; NVIS, Inc., Reston, VA). Participants' head motions were tracked with an InterSense IS-900 motion tracking system (InterSense, Inc., Billerica, MA). The virtual environment had a circular, grass-textured ground with a radius of 10,000 m (see Figure 3). The center of the virtual environment overlapped with the center of the physical room. Each participant held an InterSense IS-900 Wand (InterSense, Inc.). Analogous to moving a cursor to indicate a position by moving a mouse on a computer desktop, a virtual stick was attached to the wand so that participants could move the wand to indicate any position on the ground. White noise was presented via the HMD during the whole experiment to avoid any possible external auditory cues.

Each participant walked two experimental paths, which were the same except for the turning directions (in one case, the walker turned left, and in the other, the walker turned right). For both paths, the first (OT) and second (TP) legs were 1.8 m (see Figure 2). The turning angle was 50° for turning left and right. In the interest of brevity, we only describe the path involving a right turn in the rest of the paper. The origin (O) and the turning position (T) were indicated by red poles and the testing position (P) was indicated by a green pole (see Figure 3). The poles were 1.5 m high, with a radius of 0.05 m, and they were presented sequentially.

Participants learned the locations of five targets (ball, brush, phone, mug, and clock) and one landmark (traffic cone) before walking each path. One target was located at the origin (O in Figure 2). The other four targets (i.e., Targets 1–4 in Figure 2) were located 1.41 m from O, and 315°, 45°, 135°, and 225° clockwise with respect to the direction from O to T. The association between the targets and their positions was randomized across participants, but constant among each participant across the two paths.

The primary independent variable was the group: the consistent, conflictATwalking, and conflictAFTERwalking groups. For the consistent group, during learning, the landmark was located at the end of the path (i.e., P in Figure 2A), 1.8 m from T in the direction of 50° (clockwise for the right-turning path and counterclockwise

Table 1
Cues Determining the Estimated Testing Position (P′) According to Different Hypotheses or Based on the Observed Data in Different Experimental Conditions of Experiment 1

Experimental conditions	Retrieval-invoked resetting hypothesis	Continuous resetting hypothesis	Observed
Consistent	Idiothetic/landmark	Idiothetic/landmark	Idiothetic/landmark
ConflictATwalking	Idiothetic	Landmark	Idiothetic
ConflictAFTERwalking	Landmark	Landmark	Landmark

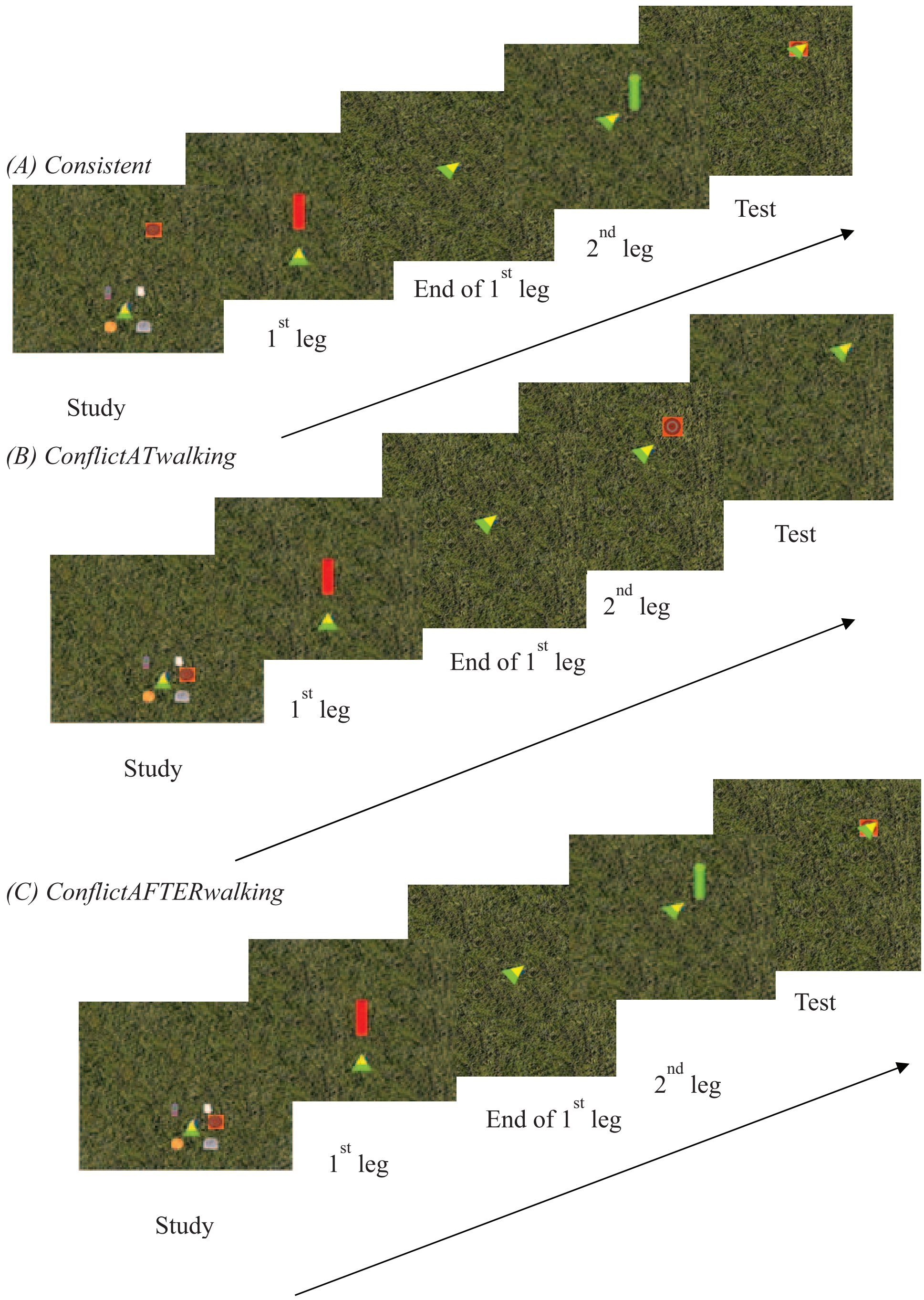

Figure 3. Timeline of Experiment 1. Participants' physical standing position is denoted by the triangle with the top part indicating participants' headings. Panel A: The condition of consistent. Panel B: The condition of conflictATwalking. Panel C: The condition of conflictAFTERwalking. See the online article for the color version of this figure.

for the left-turning path) with respect to OT (or 3.26 m from O in the direction of 25° with respect to OT. see Figure 2C for the measurements). The landmark reappeared at the original location (P) after participants walked the second leg. For the conflictATwalking and conflictAFTERwalking groups, the landmark was originally located 1.8 m from T in the direction of 150° with respect to OT (or .52 m from O in the direction of 75° with respect to OT; see Figures 2B and 2C). But it reappeared at the testing position, P, with displacement. The displaced landmark reappeared when participants started to walk the second leg and then disappeared again when participants reached the end of the second leg for the conflictATwalking group. In contrast, the displaced landmark reappeared when participants finished walking the second leg and remained presented during testing for the conflictAFTERwalking group. Participants were randomly assigned to the three groups, with an equal number of males and females in each group.

The primary dependent variable was the direction of the estimated position (OP′) at the end of the second leg. The estimated heading (H′) at the end of the second leg was also reported. The observed OP′ could indicate which cue determined the testing position in the conflictATwalking and conflictAFTERwalking groups (see details in the data analysis).

One practice path with a 90° turning angle was used prior to the two experimental paths so that participants became familiar with the experimental procedure. Different object arrays, but the same landmark, were used in the practice path.

Procedure. While wearing a blindfold, participants entered the testing room under the guidance of the experimenter. They then removed the blindfold and donned the HMD. In the virtual reality environment, they were instructed to search for and walk toward a red pole, indicating their standing position during the study (i.e., the origin, illustrated by O in Figure 2). After participants reached the pole, it disappeared. Participants were instructed to rotate in place, look for another red pole, and then face it (illustrated by T in Figure 2). This pole established participants' facing orientation in the study phase.

In the study phase, the red pole disappeared. Five targets and one landmark (a traffic cone) appeared on the ground. Participants had 3 min to learn the locations of the five targets and the landmark in the first path, and 30 s in the second path. Thirty seconds' learning in the second path was sufficient, as the five targets were in the same location, relative to participants' learning position and orientation, as in the first path. Participants only needed to learn the landmark location, which depended on the turning direction. Afterward, all targets and the landmark disappeared. Participants were requested to replace each target using the wand. The targets were probed in a random order. Feedback was given by showing the target in the correct location for 5 s. Participants needed to complete such replacing trials for two rounds to make sure that they learned these locations accurately. Then they started to walk the path.

At the beginning of walking the path, the red pole in front of the participants (illustrated by T in Figure 2) appeared again while all the targets and the landmark disappeared. After the participants reached the red pole, a green pole (illustrated by P in Figure 2) appeared. Participants turned in place to face the green pole and then walked toward it. The green pole disappeared when they reached it. In the consistent (Figure 3A) and the conflictAFTERwalking (Figure 3C) conditions, the traffic cone reappeared when participants reached the green pole. Participants were instructed to look at the landmark around their feet. Then participants replaced each probed target in a random order. The landmark was presented around participants' feet in the whole testing phase. In the conflictATwalking (Figure 3B) condition, when participants started to walk the second leg, the traffic cone was presented instead of the green pole. The landmark disappeared again when participants reached it. Participants in this group replaced the targets without the landmark. No feedback was given during this testing phase of each path. The experiment timeline for the three groups is summarized in Figure 3.

Data analysis. For each path, participants located four targets (1 to 4 in Figure 2) in addition to the origin (O in Figure 2). In total, four pairs of estimated headings (H′) and positions (OP′) were obtained, as each of the four targets (X, see Figure 1), the origin (O) and their corresponding responses (i.e., X′, O′) could lead to a pair of one estimated heading (H′) and one estimated position (OP′). For each participant and each path, we then calculated the circular mean of the four OP′s and the circular mean of the four H′s, We used the circular means of each path and each participant as the individual OP′ and H′ for further analyses mentioned in the following paragraphs.[3] As we were not interested in the influence of the turning direction while participants walked the path, the responses (OP′ and H′) for the path of the left turning were converted to and combined with those for the path of the right turning by changing the sign of the responses (OP′ and H′).

For each condition, the Rayleigh z test was used to assess whether OP′ and H′ were in random directions across participants (Batschelet, 1981). A Watson-Williams F test was used to compare the directional difference among conditions (Batschelet, 1981). The parametric test for concentration parameters was also used to examine the response variability across the conditions (Batschelet, 1981).

Most importantly, the circular means of OP′ and H′ and their confidence interval were also calculated for each condition. The 95% confidence interval (CI) of the mean was used to diagnose the cues that had determined OP′ and H′ (Batschelet, 1981). Table 2 summarizes the predictions of OP′ and H′ according to different cues. In particular, for both the conflictAFTERwalking and conflictATwalking groups, if the estimated position P′ was determined by the displaced landmark, then OP′ would be similar to the direction from the origin to the landmark's original location (O to LM in Figure 2C). If the estimated position P′ was determined by idiothetic cues, then OP′ would be the same as OP (Figure 2C). As all of the bearings (i.e., OP′ and OP) and headings (H′and H) are defined relative to the direction of OT (the first leg of the traversed path), OP′ would be 25° if it was determined by idiothetic cues, and 75° if it was determined by the landmark (see Table 2). In addition, OP′ would be 25°, indicated by both cues, for the consistent condition.

For all three conditions, if participants followed idiothetic cues, H′ would be the same as H (see Figure 2C), which was 50°. In contrast, if participants followed the landmark in the conflictATwalking condition, they thought they had turned 150° at T to face the landmark at its original location (see Figure 2C), so H′ would be 150° (the direction from T to LM in Figure 2C). As the landmark in the consistent and conflictAFTERwalking conditions was placed at each participant's testing position, it could not provide any heading information.

Results

For the interest of readers, Table 3 lists the angular values of OP, α, and H, and the circular means of α', β, OP′ and H′, for each target across participants and paths for Experiment 1. The follow-

[3] The circular correlation between the two paths for H′ or OP′ in any conditions of Experiment 1 and 2 was not significantly different from zero. This allows us to treat H′ and OP′ in the left turning and right turning paths for each individual as independent data points.

Table 2
Predictions of the Direction of the Estimated Testing Position Vector (OP′) and the Estimated Testing Heading (H′) Based on Either Cue, and the Observed OP′ and H′ in Different Experimental Conditions of Experiment 1

Experimental conditions	Prediction from idiothetic cues		Prediction from the landmark		Observed circular mean (length of mean vector, r)	
	OP′	H′	OP′	H′	OP′	H′
Consistent	25°	50°	25°	Undetermined	19° (.98)	47° (.85)
ConflictATwalking	**25°**	50°	75°	150°	37° (.88)	52° (.85)
ConflictAFTERwalking	25°	50°	**75°**	Undetermined	62° (.84)	57° (.87)

Note. The predicted OP′s consistent with the observed OP′s are in bold.

ing results were based on OP′ and H′ collapsed across targets for each participant and each path.

Angular direction of the estimated test position: OP′. OP′ for each participant and each path in all conditions is plotted in Figure 4. The circular mean values of OP′ across participants and paths, and the length of the circular means of OP′ (r), are also listed in Table 2. As illustrated in Figure 4, the means of OP′ were closer to 25° in the consistent condition and the conflictATwalking condition, and it was closer to75° in the conflictAFTERwalking condition.

The Rayleigh z test showed that the means of OP′ in all three conditions had a direction (zs ≥ 16.90, ps $< .001$). The means for OP′ in the consistent, conflictATwalking, and conflictAFTER-walking conditions were 19°, 37°, and 62°, respectively. As revealed by a Watson-Williams F test, the circular means of OP′ differed across conditions, $F(2, 69) = 15.33$, $p < .001$. Pairwise comparisons showed that the circular means of OP′ differed significantly between the consistent and conflictATwalking conditions, $F(1, 46) = 7.42$, $p = .009$, between the consistent and conflictAFTERwalking conditions, $F(1, 46) = 33.55$, $p < .001$, and between the conflictATwalking and conflictAFTERwalking conditions, $F(1, 46) = 7.52$, $p = .009$. Based on the parametric test for concentration parameters, the values of OP′ were less variable in the consistent condition than in the conflictATwalking condition, $F(23, 23) = 7.67$, $p < .001$, and in the conflictAFTERwalking condition, $F(23, 23) = 5.67$, $p < .001$, whereas the variety in the latter two did not significantly differ, $F(23, 23) = 1.35$, $p = .24$.

The confidence interval test showed that the circular mean of OP′ (19°) in the consistent condition was smaller than 25° (95% CI [14.50°, 23.88°]). The circular mean of OP′ (37°) in the conflictATwalking condition did not differ from 25° ($p > .05$), but differed from 75° ($p < .05$). These suggest that participants in the conflictATwalking condition used idiothetic cues to estimate their positions. The circular mean of OP′ (62°) in the conflictAFTER-walking condition did not differ from 75° ($p > .05$), but differed from 25° ($p < .05$). These suggest that participants in the conflictAFTERwalking group used the landmark to estimate their positions.

Angular direction of the estimated test heading: H′. H′ for each participant and each path in all conditions is plotted in Figure 5. The circular means of H′ and the length of the circular means of H′ (r) are also listed in Table 2. As illustrated in Figure 5, the means of H′ were close to 50° in all three conditions.

The Rayleigh z test showed that the values of H′ in all conditions had one direction (zs ≥ 17.50, ps $< .001$). The means for H′ in the consistent, conflictATwalking, and conflictAFTERwalking conditions were 47°, 52°, and 57°, respectively. Neither the circular mean of H′ nor the variability of the values of H′ were significantly different across conditions (Watson-Williams F test, $F[2, 69] = .54$, $p = .58$; parametric test, Fs ≥ 1.08, ps $\geq .43$).

The confidence interval test showed that none of the circular means of H′ in the three conditions differed from 50° (ps $> .05$). For the conflictATwalking condition, the circular mean of H′ was significantly different from 150° ($p < .05$). These indicate that

Table 3
OP, α, and H, and the Observed Circular Means (Length of the Mean Vectors, R) of α′, β, OP′, and H′ Across Participants and Paths for Each Target and Each Experimental Condition in Experiment 1

Experimental conditions	Target object	OP	α	H	α′	β	OP′	H′
Consistent	Target 1	25°	110°	50°	108° (.86)	357° (.90)	26° (.86)	53° (.70)
	Target 2	25°	200°	50°	214° (.86)	357° (.90)	11° (.86)	37° (.79)
	Target 3	25°	290°	50°	296° (.94)	357° (.90)	19° (.94)	47° (.88)
	Target 4	25°	20°	50°	25° (.92)	357° (.90)	20° (.92)	49° (.78)
ConflictATwalking	Target 1	25°	110°	50°	92° (.88)	10° (.88)	43° (.88)	58° (.76)
	Target 2	25°	200°	50°	185° (.83)	10° (.88)	40° (.83)	55° (.76)
	Target 3	25°	290°	50°	275° (.80)	10° (.88)	40° (.80)	53° (.79)
	Target 4	25°	20°	50°	21° (.65)	10° (.88)	24° (.65)	42° (.75)
ConflictAFTERwalking	Target 1	25°	110°	50°	67° (.70)	25° (.70)	68° (.70)	53° (.71)
	Target 2	25°	200°	50°	159° (.90)	25° (.70)	66° (.90)	63° (.80)
	Target 3	25°	290°	50°	248° (.79)	25° (.70)	67° (.79)	62° (.80)
	Target 4	25°	20°	50°	353° (.63)	25° (.70)	52° (.63)	45° (.81)

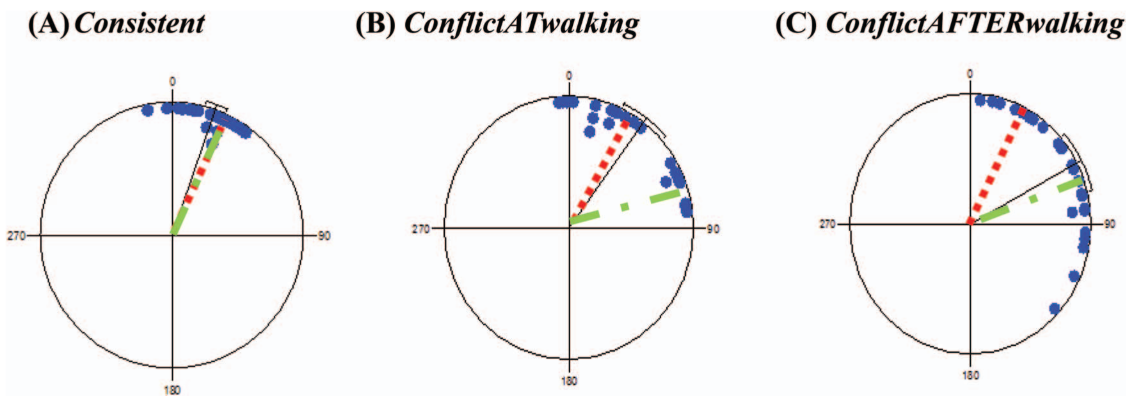

Figure 4. Observed and predicted angular directions of the estimated testing position (OP′) in the consistent condition (Panel A), the conflictATwalking condition (Panel B), and the conflictAFTERwalking condition (Panel C) in Experiment 1. Each blue dot indicates one observed OP′ of one path of one participant (the signs of OP′ for the path with the left turn are converted by changing the sign). The solid black line indicates the circular mean of the observed OP′s. The arc above the mean direction indicates the 95% confidence interval of the mean direction of the observed OP′s. The dotted red line indicates the predicted direction of OP′ following idiothetic cues (25°). The dashed green line indicates the predicted direction of OP′ following the landmark: 75° for the conflictATwalking and the conflictAFTERwalking conditions, and 25° for the consistent condition. See the online article for the color version of this figure.

participants in all conditions used idiothetic cues to estimate their testing headings.

Discussion

The results of this experiment showed that when the displaced landmark was presented while participants were walking the second leg, but not during the testing phase, they used idiothetic cues to estimate their positions. In contrast, when the displaced landmark was presented after walking and in the testing phase, participants used the displaced landmark to estimate their positions. Therefore, the results of Experiment 1 favored the retrieval-invoked resetting hypothesis over the continuous resetting hypothesis, as participants did not continuously use the piloting system to estimate their positions. The results showed that in all three conditions, participants relied on the path integration system to estimate their headings regardless of the displaced landmark.

One may argue that participants reset their positions in the conflictAFTERwalking condition, but not in the conflictATwalking condition, because the displaced landmark provided no orientation information in the former condition but conflicting orientation information in the latter one. Participants in the conflictATwalking condition did not reset their positions because

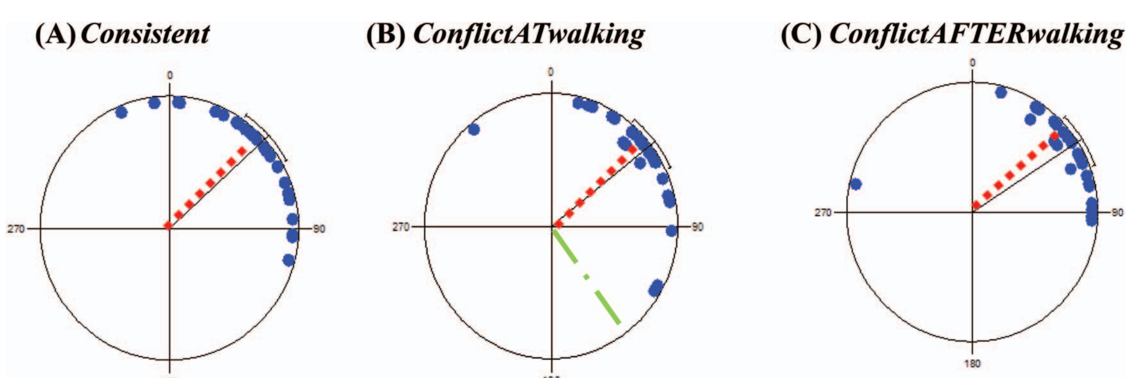

Figure 5. Observed and predicted angular directions of the estimated testing heading (H′) in the consistent condition (Panel A), the conflictATwalking condition (Panel B), and the conflictAFTERwalking condition (Panel C) in Experiment 1.Each blue dot indicates one observed H′ for one path of one participant (the signs of H′ for the path with the left turn are converted by changing the sign). The solid black line indicates the circular mean of the observed H′s. The arc above the mean direction indicates the 95% confidence interval of the mean direction of the observed H′s. The dotted red line indicates the predicted direction of H′ following idiothetic cues (50°). The dashed green line indicates the predicted direction of H′ following the landmark for the conflictATwalking condition (150°). The landmark cannot provide the heading information for either the conflictAFTERwalking or the consistent conditions. See the online article for the color version of this figure.

they might have noticed the conflict orientation information and then might have ignored the displaced landmark. Experiment 2 addressed this issue to further differentiate the retrieval-invoked resetting hypothesis from the continuous resetting hypothesis. Furthermore, Experiment 2 was also designed to differentiate the retrieval-invoked resetting hypothesis from the combination without resetting hypothesis by investigating whether the path integration system uses the position corrected by the piloting system as the initial position of a new movement, even when the piloting cue is not available during the new movement.

Experiment 2

One purpose of Experiment 2 was to differentiate between the retrieval-invoked resetting hypothesis and the combination without resetting hypothesis. This was accomplished by asking people, without seeing the piloting cue, to start a new movement after walking a 2-leg path. We wanted to see whether participants would use the position estimated by the path integration system as the initial position, or whether they would use the position that had been corrected by the piloting system. The other purpose of Experiment 2 was to further differentiate between the retrieval-invoked resetting hypothesis and the continuous resetting hypothesis by removing the conflict heading information provided by the displaced landmark in the conflictATwalking condition of Experiment 1.

Three groups of participants were included in this experiment. For all groups, after walking the 2-leg path (O-T-T2 in Figure 6 and Figure 7) used in Experiment 1, participants further walked a third leg (T2-P in Figure 6 and Figure 7). Two groups of participants, similar to the conflictAFTERwalking group in Experiment 1, saw the displaced landmark at their position when they reached the end of the second leg (T2 in Figure 6B and Figure 7). One of these two groups (the *3-leg inconsistent pointing* group) pointed to one target before they walked the third leg. The other group (the *3-leg inconsistent no-pointing* group) did not point to any target before walking the third leg. The last group, similar to the consistent group in Experiment 1, saw the landmark at the end of the second path when they learned the targets and when they reached the end of the second leg. This group provided the baseline position estimation.

The retrieval-invoked resetting hypothesis differs from the combination without resetting hypothesis in the prediction about the cue determining the initial position of the third leg in the 3-leg inconsistent pointing group (see Table 4). The retrieval-invoked resetting hypothesis stipulates that once the piloting system overrides the estimated position in the path integration system, the path integration system uses the overridden position as the initial position of a further movement. Therefore, participants in the 3-leg inconsistent pointing group would use the landmark to determine the initial position of the third leg. In contrast, the combination without resetting hypothesis stipulates that the path integration system and the piloting system work independently and contribute to position estimations by a weighted average. For any new movement without the piloting cues, the path integration system uses its own estimated position rather than the corrected position as the initial position of the new movement. Therefore, this hypothesis predicted that participants in the 3-leg inconsistent pointing group would use idiothetic cues to determine the initial position of the third leg.

The continuous resetting hypothesis and the retrieval-invoked resetting hypothesis have different predictions about the cues used to determine the initial position of the third leg in the 3-leg inconsistent no-pointing group and the 3-leg inconsistent pointing group (see

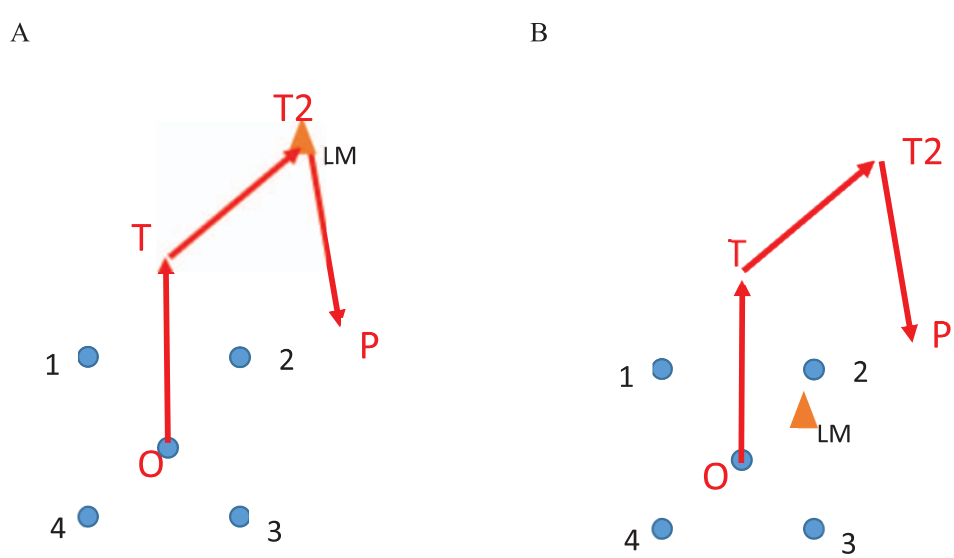

Figure 6. Schematic diagram of the experimental setup in Experiment 2. The 3-leg path includes the origin (O), the turning point (T and T2), and the ending position (P). All the targets, the landmark, and the path are presented together only for readers. Five dots are denoted as five targets (one is placed at the origin, and the other four are numbered as 1–4). The triangle is denoted as the landmark (LM). In the 3-leg consistent condition, the landmark was placed at the turning point T2 (Panel A). In the 3-leg inconsistent no-pointing and 3-leg inconsistent pointing conditions, the landmark was originally placed at one other location (Panel B). See the online article for the color version of this figure.

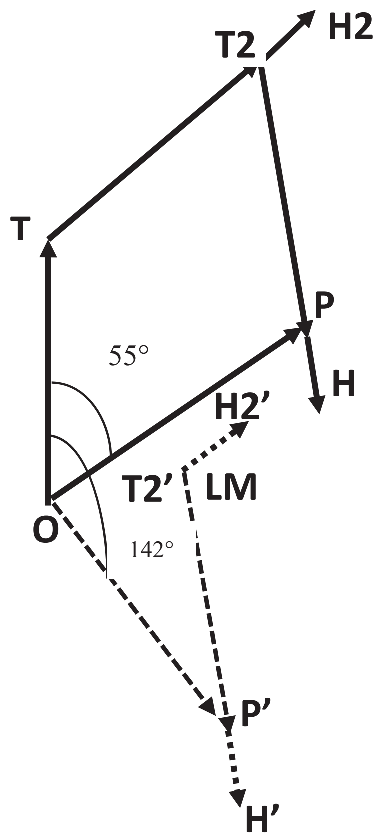

Figure 7. Illustration of the position and heading estimations in the 3-leg inconsistent no-pointing and 3-leg inconsistent pointing conditions. Participants walked from O to T (1.8 m), turned 50° right from T to T2 (1.8 m), and walked to T2. They then saw the displaced landmark, turned 120° right from T2 to P (1.8 m), and walked to P. H2 is the heading at the end of the second leg. H is the testing heading. If the initial position of the third leg was determined by the landmark, when participants walked the third leg (T2P), they would act as if they walked from T2′, the original location of the landmark (LM), to P′. T2′P′ equals T2P with respect to both the direction and length. The estimated testing heading H′ equals H. If the initial position of the third leg was determined by idiothetic cues, participants' estimated testing position and heading would be the same as the actual testing position (P) and heading (H).

Table 4). The continuous resetting hypothesis predicted that the resetting process would occur in both groups. Therefore, participants would use landmarks to estimate their positions in both groups. However, the retrieval-invoked resetting hypothesis stipulates that the resetting occurs when people have to judge their positions in an environment in the presence of the conflicting piloting cues. Therefore, people in the 3-leg inconsistent pointing group would use the landmark to estimate their positions and the resetting would occur, because participants pointed to one target in the presence of the displaced landmark. However, people in the 3-leg inconsistent no-pointing group would use idiothetic cues to judge their positions and the resetting would not occur because they did not point to any target in the presence of the displaced landmark. Furthermore, as participants in both groups saw the displaced landmark at their position, the expectation was that the landmark would not be a conflicting heading cue in either group. Consequently, there would be a more marked difference between the continuous resetting hypothesis and the retrieval-invoked resetting hypothesis in this experiment than in Experiment 1.

Table 4 lists the cues determining the estimation of the initial position of the third leg according to these three hypotheses in all three groups. For the *3-leg consistent* group, both idiothetic cues and the landmark indicate the same position according to all hypotheses.

Method

Participants. Thirty-six university students (18 men and 18 women) participated in this experiment to fulfill the partial requirement for an introductory psychology course.

Materials, design, and procedure. All participants walked two experimental paths (one left and one right). The first two legs of the path were the same as those in Experiment 1. The second turning angle was 120° in the same direction as the first turning direction (see the right turn case in Figure 6). The length of the third leg was 1.8 m as well.

The primary independent variable was the group: the 3-leg consistent, 3-leg inconsistent no-pointing, and 3-leg inconsistent pointing groups. The 3-leg consistent group was identical to the consistent group in Experiment 1, except that participants in the 3-leg consistent group walked the third leg (Figure 6A). They learned the location of the landmark being placed at the end of the second leg (i.e., T2 in Figure 6A), and then, after walking the 2-leg path (O-T-T2 in Figure 6A), saw the landmark at the same location. Without viewing the landmark, they walked one more leg (from T2 to P), and then pointed to the five targets. The 3-leg inconsistent no-pointing group and the 3-leg inconsistent pointing group were identical to the conflictAFTERwalking group of Experiment 1, except that participants in these two groups walked the third leg (Figure 6B). In the study phase, they learned the landmark location being placed at 1.8 m from T in the direction of 150° (or .52 m from O in the direction of 75°), with respect to OT (Figure 6B), and then, after walking a 2-leg path (O-T-T2 in Figure 6B), viewed the displaced landmark presented around their feet (at T2).

Table 4
Cues Determining the Initial Position of the Third Leg According to Different Hypotheses or Based on the Observed Data in Different Experimental Conditions of Experiment 2

Experimental conditions	Retrieval-invoked resetting hypothesis	Continuous resetting hypothesis	Combination without resetting hypothesis	Observed
3-leg consistent	Idiothetic/landmark	Idiothetic/landmark	Idiothetic/landmark	Idiothetic/landmark
3-leg inconsistent no-pointing	Idiothetic	Landmark	Idiothetic	Idiothetic
3-leg inconsistent pointing	Landmark	Landmark	Idiothetic	Landmark

Without viewing the landmark, they walked one more leg (from T2 to P) and then pointed to the five targets. There was only one difference between the 3-leg inconsistent no-pointing group and the 3-leg inconsistent pointing group. It was that before participants walked the third leg, in the presence of the displaced landmark, the former group did not point to any target, whereas the latter group was asked to replace one of the four targets excluding the one at the origin. Participants were randomly assigned to the three groups with an equal number of males and females in each group.

The primary dependent variable was the direction of the estimated position (OP′) at the end of the third leg. The estimated heading (H′) at the end of the third leg was also reported. In all groups, H′ was expected to be the same as H (170°), as participants could only rely on idiothetic cues to determine their headings. This was the case even for the group that saw the displaced landmark at the end of the second leg; because the displaced landmark was placed at each participant's position, it could not provide any heading information. The finding of Experiment 1 also confirmed that the displaced landmark that was placed at each participant's position did not change the heading estimated by the path integration system, although it reset the position estimation in the path integration system. Therefore, H′ should be the same as that estimated by the path integration system (see Figure 7 and Table 5). The observed H′ could then examine how accurately participants used idiothetic cues to determine their headings after walking a 3-leg path.

The observed OP′ could indicate which cue determined the estimated initial position of the third leg. In particular, for the 3-leg consistent group, OP′ was expected to be 55° (same as the OP, Figure 7) regardless of which cue determined the initial position of the third leg. For the 3-leg inconsistent no-pointing group and 3-leg inconsistent pointing group, if the initial position of the third leg was determined by idiothetic cues, then OP′ would be the same as that in the 3-leg consistent condition (i.e., 55°). In contrast, if the initial position of the third leg was determined by the displaced landmark, participants would think that they departed at the original position of the landmark (T2′ or LM in Figure 7) and walked 1.8 m in the direction from T2 to P (the same as the direction from T2′ to P′ in Figure 7). Therefore, the ending position would be the same as P′ illustrated in Figure 7. OP′ would be expected to be 142° (see Figure 7). The predictions of OP′ and H′ determined by different cues in different groups are summarized in Table 5.

The procedures were the same as in Experiment 1, with the exception of the following changes. After participants walked the second leg, they were instructed to see the landmark that reappeared around their feet. For the 3-leg consistent and 3-leg inconsistent no-pointing conditions, after participants viewed the landmark for 5 s, they walked the third leg by walking toward a new pole. After finishing the third leg, they pointed at all targets. For the 3-leg inconsistent pointing condition, participants were asked to replace the target probed on the screen before walking the third leg. This target was randomly chosen from the targets other than the one at the origin. No feedback was provided. After finishing the third leg, participants pointed at all targets. The experiment timeline for the three groups is summarized in Figure 8.

Results

For the interest of readers, Table 6 lists the angular values of OP, α, and H, and the circular means of α', β, OP′, and H′ for each target across participants and paths. The following results were based on the circular means of OP′ and H′ collapsed across targets for each participant and each path.

Angular direction of the estimated test position: OP′. The values of OP′ in all of the conditions are plotted in Figure 9. The means of OP′ and the length of the means of OP′ (r) are also listed in Table 5. As illustrated in Figure 9, the mean of OP′ was closer to 55° in both the 3-leg consistent and the 3-leg inconsistent no-pointing conditions, and closer to 142° in the 3-leg inconsistent pointing condition.

The Rayleigh *z* test showed that the means of OP′ in all conditions had one direction (zs ≥ 5.43, ps $\geq .004$). The means of OP′ in the 3-leg consistent, 3-leg inconsistent no-pointing, and 3-leg inconsistent pointing conditions were 51°, 65°, and 119°, respectively. As revealed by a Watson-Williams *F* test, the circular mean of OP′ in the 3-leg inconsistent pointing condition differed significantly from the other two, Fs $(1, 46) \geq 6.83$, ps $\geq .012$, whereas the other two did not differ, $F(1, 46) = 0.75$, $p = .39$. The values of OP′ were less variable in the 3-leg consistent condition than in the other two conditions, Fs $(23, 23) \geq 3.84$, ps $\geq .001$, whereas those in the other two conditions did not differ, $F(23, 23) = .86$, $p = .64$.

According to the confidence interval test, neither of the circular means of OP′ in the 3-leg consistent and 3-leg inconsistent no-pointing conditions differed from 55° (ps $> .05$), but both differed from 142° (ps $< .05$). These results indicate that participants in the 3-leg inconsistent no-pointing condition used idiothetic cues to judge their positions. However, the circular mean of OP′ for the 3-leg inconsistent pointing condition did not differ from 142° ($p > .05$), but differed from 55° ($p < .05$). These indicate that participants in the 3-leg inconsistent pointing condition used the landmark to reset their

Table 5
Predictions of the Direction of the Estimated Testing Position Vector (OP′) and the Estimated Testing Heading (H′) Based on Either Cue, and the Observed Circular Means and the Mean Length in Different Experimental Conditions of Experiment 2

Experimental conditions	Prediction from idiothetic cues		Prediction from the landmark		Observed circular mean (length of mean vector, r)	
	OP′	H′	OP′	H′	OP′	H′
3-leg consistent	55°	170°	55°	undetermined	51° (.88)	175° (.89)
3-leg inconsistent no-pointing	**55°**	170°	142°	undetermined	65° (.48)	205° (.66)
3-leg inconsistent pointing	55°	170°	**142°**	undetermined	119° (.55)	197° (.54)

Note. The predicted OP′s consistent with the observed OP′s are in bold.

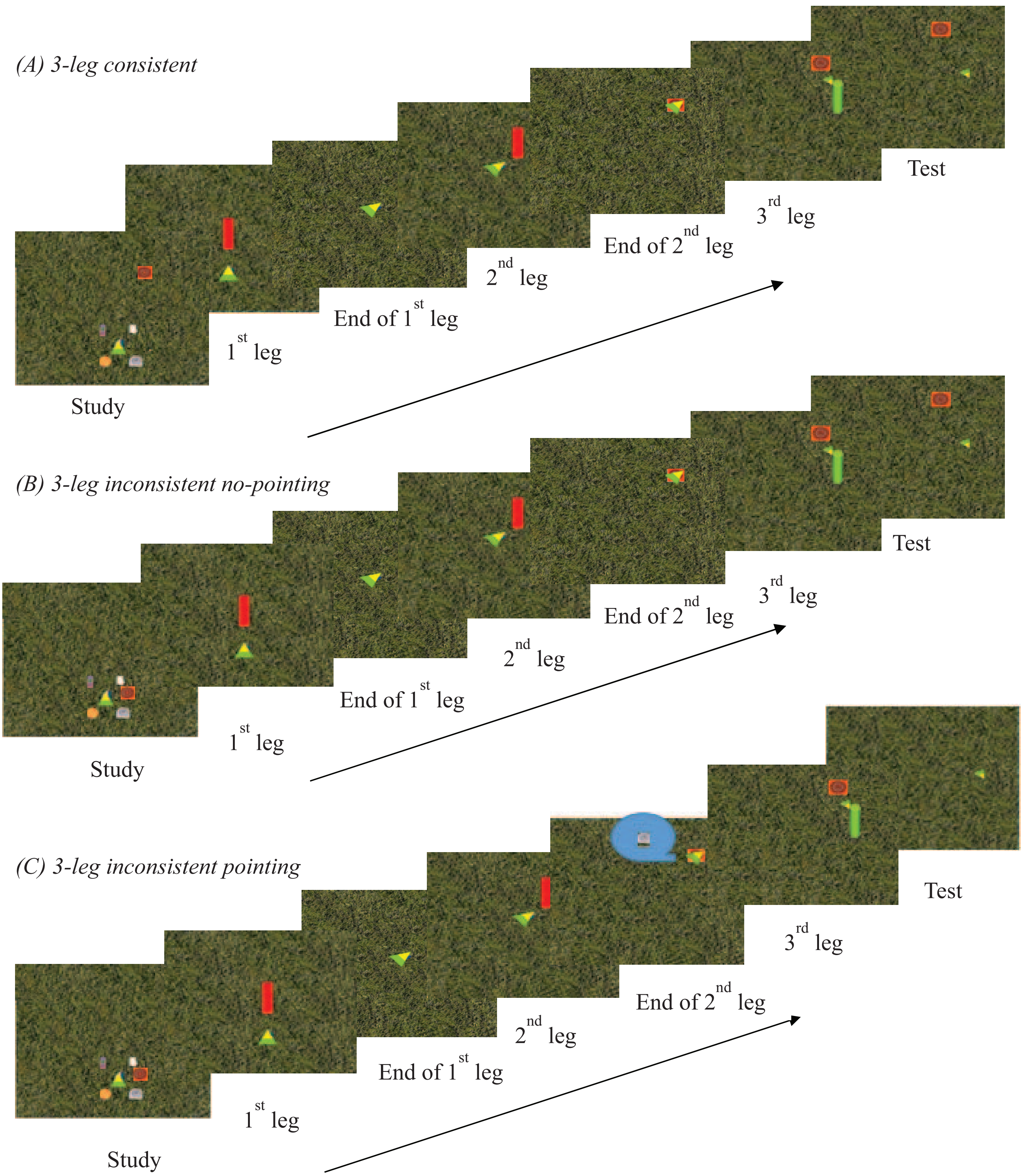

Figure 8. Timeline of Experiment 2. Participants' physical standing position is denoted by the triangle with the top part indicating participants' headings. Panel A: The condition of 3-leg consistent. Panel B: The condition of 3-leg inconsistent no-pointing. Panel C: The condition of 3-leg inconsistent pointing. The blue bubble in the "End of 2nd leg" indicated that participants had to point to one object at the end of 2nd leg. This object was randomly chosen from the four objects except for the one in the origin. See the online article for the color version of this figure.

Table 6
OP, α, and H, and the Observed Circular Means (Length of the Mean Vectors, R) of α′, β, OP′, and H′ Across Participants and Paths for Each Target and Each Experimental Condition in Experiment 2

Experimental conditions	Target object	OP	α	H	α′	β	OP′	H′
3-leg consistent	Target 1	55°	80°	170°	79° (.82)	354° (.72)	56° (.82)	182° (.80)
	Target 2	55°	170°	170°	183° (.79)	354° (.72)	42° (.79)	168° (.79)
	Target 3	55°	260°	170°	257° (.82)	354° (.72)	58° (.82)	183° (.85)
	Target 4	55°	350°	170°	358° (.83)	354° (.72)	47° (.83)	172° (.70)
3-leg inconsistent no-pointing	Target 1	55°	80°	170°	72° (.44)	10° (.40)	63° (.44)	209° (.54)
	Target 2	55°	170°	170°	160° (.53)	10° (.40)	65° (.53)	208° (.70)
	Target 3	55°	260°	170°	241° (.42)	10° (.40)	74° (.42)	202° (.54)
	Target 4	55°	350°	170°	343° (.27)	10° (.40)	62° (.27)	203° (.59)
3-leg inconsistent pointing	Target 1	55°	80°	170°	10° (.33)	59° (.76)	125° (.33)	192° (.32)
	Target 2	55°	170°	170°	108° (.49)	59° (.76)	117° (.49)	197° (.60)
	Target 3	55°	260°	170°	195° (.67)	59° (.76)	120° (.67)	189° (.63)
	Target 4	55°	350°	170°	286° (.48)	59° (.76)	119° (.47)	190° (.49)

positions at the end of the second leg, and participants carried this reset position to the third leg even when the landmark was not available.

Angular direction of the estimated test heading: H′. The values of H′ in all conditions are plotted in Figure 10. The means of H′ and the length of the means of H′ (r) are also listed in Table 5. As illustrated in Figure 10, the means of H′ were close to 170°.

The Rayleigh *z* test showed that the values of H′ in all conditions had one direction ($zs \geq 7.06$, $ps < .001$). The means of H′ for the 3-leg consistent, 3-leg inconsistent no-pointing and 3-leg inconsistent pointing conditions were 175°, 205°, and 197°, respectively. As revealed by a Watson-Williams *F* test, the difference between the 3-leg consistent and 3-leg inconsistent no-pointing conditions was significant, $F(1, 46) = 5.84$, $p = .02$, whereas the difference between other two pairs was not, $Fs\ (1, 46) \leq 2.31$, $ps \leq .66$. The values of H′ were less variable in the 3-leg consistent condition than in the other two conditions, $Fs\ (23, 23) \geq 3.19$, $ps \geq .004$, whereas the variety in the other two conditions did not differ significantly, $F(23, 23) = 1.34$, $p = .24$.

As shown by the confidence interval test, neither of the circular means of H′ in the 3-leg consistent condition and the 3-leg inconsistent pointing condition differed significantly from 170° ($ps > .05$). The circular mean of H′ in the 3-leg inconsistent no-pointing condition was significantly different from 170° ($p < .05$), although it was close to 170° (95% CI [183.63°, 225.97°]).

Discussion

The results showed that in the 3-leg inconsistent pointing condition, the displaced landmark determined the estimated initial position of the third leg. It indicates that the visual landmark resets the position estimation in the path integration system and this

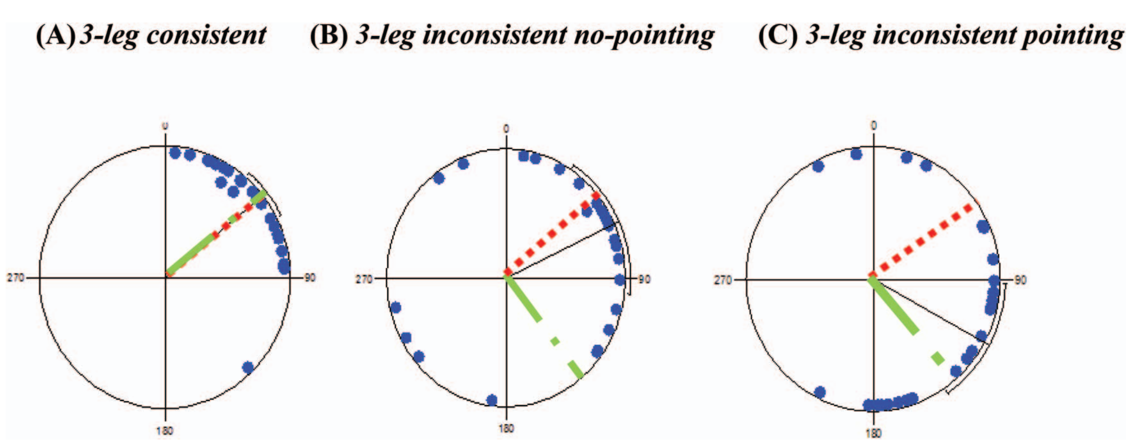

Figure 9. Observed and predicted angular directions of the estimated testing position (OP′) in the 3-leg consistent condition (Panel A), the 3-leg inconsistent no-pointing condition (Panel B), and the 3-leg inconsistent pointing condition (Panel C) in Experiment 2. Each blue dot indicates the observed OP′ of one path of one participant (the signs of OP′ for the path with the left turn are converted by changing the sign). The solid black line indicates the circular direction of the observed OP′s. The arc above the mean direction indicates the 95% confidence interval of the mean direction of the observed OP′s. The dotted red line indicates the predicted direction of OP′ following idiothetic cues (55°). The dashed green line indicates the predicted direction of OP′ following the landmark cue: 142° for the 3-leg inconsistent no-pointing and 3-leg inconsistent pointing conditions, and 55° for the 3-leg consistent condition. See the online article for the color version of this figure.

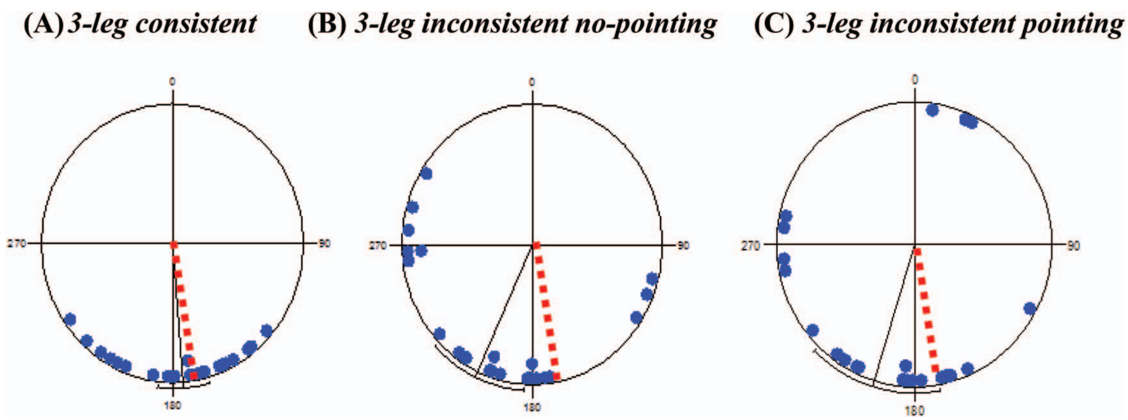

Figure 10. Observed and predicted angular directions of the estimated testing heading (H′) in the 3-leg consistent condition (Panel A), the 3-leg inconsistent no-pointing condition (Panel B), and the 3-leg inconsistent pointing condition (Panel C) in Experiment 2. Each blue dot indicates the observed H′ of one path of one participant (the signs of H′ for the path with the left turn are converted by changing the sign). The solid black line indicates the circular mean of the observed H′s. The arc above the mean direction indicates the 95% confidence interval of the mean direction of the observed H′s. The dotted red line indicates the predicted direction of H′ following idiothetic cues (170°). See the online article for the color version of this figure.

system carries this reset position in a new movement. Hence, this finding favored the retrieval-invoked resetting hypothesis over the combination without resetting hypothesis. Furthermore, the results showed that resetting occurred when participants were asked to judge their positions (3-leg inconsistent pointing condition), but did not occur when participants were not asked to judge their positions (3-leg inconsistent no-pointing condition). This result favored the retrieval-invoked resetting hypothesis over the continuous resetting hypothesis even after we removed any conflicting heading information provided by the displaced landmark.

General Discussion

The purpose of this project was to investigate how the piloting system and the path integration system interact in estimating positions during human navigation. There are two important findings. First, participants ignored the displaced landmark and used idiothetic cues to determine their positions when they were not explicitly required to judge their positions in the presence of the displaced landmark. In contrast, the displaced landmark overrode idiothetic cues in the position estimation when participants were explicitly required to judge their positions in the presence of the displaced landmark. Also, if the displaced landmark overrode idiothetic cues, the path integration system used the corrected position as the initial position of the new movement when the displaced landmark was no longer available.

These findings differentiated the retrieval-invoked resetting hypothesis from the continuous resetting hypothesis and the combination without resetting hypothesis. The retrieval-invoked resetting hypothesis is derived from the prevailing theory that has two key claims. First, the path integration system dynamically updates one's position, and the piloting system intermittently corrects the error accumulated in the path integration system (Etienne et al., 2004; Gallistel, 1990; Müller & Wehner, 1988). Second, once the piloting system corrects the errors of the estimated position in the path integration system, the path integration system uses the corrected position as the initial position of the next new movement (Etienne et al., 2004). The retrieval-invoked resetting hypothesis further constrains the prevailing theory by proposing that the piloting system resets the path integration system when people need to determine their positions in the presence of the conflicting piloting cues. When people determine their positions, they retrieve their position representations produced by the path integration system and by the piloting system. If these two representations differ significantly, the piloting system might reset the path integration system.

The continuous resetting hypothesis differs from the retrieval-invoked resetting hypothesis in terms of the claim that the piloting system intermittently resets the path integration system. The continuous resetting hypothesis is inspired by the idea that when idiothetic cues and visual cues are both available to a navigator, they dynamically contribute to an integrated position representation (e.g., Tcheang et al., 2011). Therefore, according to the continuous resetting hypothesis, the piloting system might continuously reset the path integration system whenever the piloting cues are available.

The combination without resetting hypothesis differs from the retrieval-invoked resetting hypothesis in terms of the claim that the path integration system uses the position corrected by the piloting system as the start of a new movement even when the piloting cue is not available. The combination without resetting hypothesis is based on the cue combination models in spatial navigation (Chen & McNamara, 2014; Cheng et al., 2007; Nardini et al., 2008; Zhao & Warren, 2015a). According to the key assumption of the cue combination models, although people average the position representations produced by the piloting system and the path integration system, the individual representation in either system is intact. Therefore, according to the combination without resetting hypothesis, although piloting cues and idiothetic cues could be combined to determine locations, the path integration system uses its own position representation as the initial position of any new movement when piloting cues are removed.

The first finding in the current study is that the displaced landmark, presented when participants were required to determine their positions, overrode idiothetic cues in humans' position estimation. This finding favors the retrieval-invoked resetting hypothesis over the continuous resetting hypothesis. In Experiment 1, when the displaced landmark was presented while participants were walking the second leg (conflictATwalking), participants used idiothetic cues rather than the displaced landmark to estimate their positions. In contrast, participants' position estimation was determined by the displaced landmark that was presented when participants pointed to targets (conflictAFTERwalking). These results indicate that whether the displaced landmark overrode idiothetic cues depended on whether participants were required to determine their positions. The retrieval-invoked resetting hypothesis readily explains these results. In contrast, it is difficult for the continuous resetting hypothesis to explain why resetting depended on when participants saw the displaced landmark. If the piloting system had reset the path integration system whenever the conflicting piloting cues were available, resetting would have occurred in both conditions.

There might be a different way to explain why resetting occurred in the conflictAFTERwalking condition but not in the conflictATwalking condition in Experiment 1. In the conflictAFTERwalking condition, the displaced landmark generated a mismatch only in the position, but not in the heading, as the displaced landmark was at the participants' own location. In contrast, in the conflictATwalking condition, the displaced landmark was away from participants; thus, it generated a mismatch in the heading as well as in the position. In particular, the displaced landmark indicated that participants should have turned 150° to see the landmark at its original location, whereas idiothetic cues indicated that participants had turned 50°. This suggests that the different results between the conflictAFTERwalking and conflictATwalking conditions might have been resulted from the difficulty in resetting the heading in the conflictATwalking condition, and not from how each participant judged their positions in the presence of the displaced landmark in the conflictAFTERwalking condition.

This concern was addressed in Experiment 2. In both the 3-leg inconsistent no-pointing and the 3-leg inconsistent pointing conditions, the displaced landmark was presented at the participants' own location when they finished walking the second leg. Therefore, the displaced landmark only generated a mismatch in the position, but not in the heading in both conditions. The only difference between these two conditions was that participants in the 3-leg inconsistent pointing condition were required to point to a target using their memory, whereas participants in the 3-leg inconsistent no-pointing condition were not required to point. The results showed that the displaced landmark in the 3-leg inconsistent pointing condition, but not in the 3-leg inconsistent no-pointing condition, overrode idiothetic cues in the position estimation. This confirmed the retrieval-invoked resetting hypothesis.

The second finding of the current study is that participants could use the position corrected by the landmark as the initial position of the third leg in the 3-leg inconsistent pointing condition. This finding supports the retrieval-invoked resetting hypothesis rather than the combination without resetting hypothesis. When participants started to walk the third leg, the displaced landmark was not available. According to the retrieval-invoked resetting hypothesis, because the displaced landmark overrode idiothetic cues in humans' position estimations at the end of the second leg, the path integration system would use the corrected position as the starting position of the third leg. In contrast, according to the combination without resetting hypothesis, the path integration system would have used the position representation in its own system as the start of the third leg, because the piloting cue was no longer available during the third leg.

The findings of the current project provide clear evidence confirming the two key claims of the prevailing theory (Etienne et al., 2004; Gallistel, 1990; Müller & Wehner, 1988). It has been reported that the piloting system could override the path integration system in humans' heading estimations (e.g., Mou & Zhang, 2014; Zhao & Warren, 2015a, 2015b). The evidence supporting that the piloting system could override the path integration system in humans' position estimations, however, is rare. Furthermore, the current study provides a novel demonstration that even when the piloting cues are no longer available, the path integration system uses the corrected position in the piloting system as the initial position of a new movement. Etienne et al. (2004) reported a similar finding in hamsters. However, to our knowledge, there was no such demonstration in human navigation. Most importantly, the current findings also constrain the prevailing theory by showing that whether the piloting cues (the displaced landmark) reset the path integration system depends on whether participants were required to judge their positions in the presence of the conflicting piloting cues.

This retrieval-invoked resetting hypothesis indicates that in humans, the piloting system might not spontaneously reset the path integration system. People might need to be motivated to detect the discrepancy between their position representations produced by the piloting system and by the path integration system. For example, even though familiar landmarks are available to both the driver of a local bus and the passengers, the driver may be more likely than the passengers to reset his or her position using visual landmarks because drivers are more motivated to do so. We acknowledge that explicitly requiring participants to judge their positions in the presence of a displaced landmark, as we did in the current study, is just one way to motivate participants to detect the discrepancy between the position representations in these two systems. People might compare their position representations produced by these two systems when they realize that the errors in the path integration system are accumulated substantially after walking a relatively long circuitous path. Kelly, McNamara, Bodenheimer, Carr, and Rieser (2008) have shown that an angular room can remove errors accumulating in the path integration system, especially when people walk a path with six legs.

Although the findings of the current study do not support the continuous resetting hypothesis, we do not conclude that people cannot form a multimodal representation of the path as proposed by Tcheang and colleagues (2011). Participants in their study might indeed have formed such representations. However, we conjecture that people might integrate both visual cues and inertial cues within the path integration system to form these representations. As visual cues could also indicate participants' moving direction and moving speed (acting as optical flow, e.g., Klatzky et al., 1998), the path integration system could dynamically use visual cues (optical flow) as well as inertial cues to estimate the position and the heading. For example, Warren et al. (2001) showed that optical flow could override inertial cues in determining headings. Therefore, visual cues in Tcheang et al.'s study might have been processed by the path integration system rather than by the piloting system. Similarly, although the findings of the current study do not support the combination without resetting hypothesis, we do not conclude that people cannot combine cues as demonstrated by studies of the cue combination in human navigation (Cheng et al., 2007; Nardini et al., 2008; but see Foo, Warren, Duchon, & Tarr, 2005; Zhao & Warren, 2015a). Some participants, even in the current project, might have combined cues to estimate positions. Instead, importantly, we conclude in the current project that the position representation in the path integration system might be modified by the separate position representation in the piloting system.

One finding of the current study strikingly mirrored the finding in our previous study (Mou & Zhang, 2014). The results of the previous study showed that when the orientation cue was presented during walking, participants ignored the rotated orientation cue and relied on idiothetic cues to estimate their headings. However, the rotated orientation cue overrode idiothetic cues when the orientation cue was presented after walking and during testing. In the current study, a similar pattern was observed when participants estimated their positions. Therefore, the retrieval-invoked resetting hypothesis can also be applied to human heading as well as position estimations.

The current study showed that although participants' position estimations might be determined by the displaced landmark, their heading estimation was determined by idiothetic cues. This finding also mirrored the previous findings that although the heading estimation was determined by the rotated orientation cues, the position estimation was determined by idiothetic cues (Mou & Zhang, 2014). Our previous study and the current one together demonstrate the heading or position representation in the path integration system can be reset selectively by rotated orientation cues or by a displaced landmark when people retrieve their headings or positions in the presence of the piloting cues. These findings echo the findings of separate codes for head direction and place in neuroscience (Ekstrom et al., 2003; Jacobs, Kahana, Ekstrom, Mollison, & Fried, 2010; Jeffery, 2007; O'Keefe & Dostrovsky, 1971; Taube, 2007; Vass & Epstein, 2013). We acknowledge that the reset heading representation will affect the position estimation in the path integration system when people resume their locomotion (Aghajan et al., 2015).

One limitation of the current project was that each participant only walked two experimental paths. It is hard to tell whether the variance in the position estimation is from individual differences of the resetting process or only from experimental noises. In particular, although the analyses based on the group mean of OP′ indicated that, in general, participants used retrieval-invoked resetting process, it is likely that some participants might have used the continuous resetting process. In Experiment 1, the mean OP′ in the conflictATwalking condition differed from that in the consistent condition, indicating that some participants in the conflictATwalking condition might have reset their positions even without being asked to determine their positions. It is also likely that some participants who had been asked to determine their positions might not have reset their positions, suggested by the result that the variance in the conflictAFTERwalking condition was larger than that in the consistent condition in Experiment 1. Similarly it is also possible that some participants might only have combined different cues but never reset the path integration system using the piloting cues, indicated by the larger variance in the 3-leg inconsistent pointing condition than in the 3-leg consistent condition.

One other limitation of the current project was that we used a small and movable object (i.e., traffic cone) as a landmark. The likelihood of the participants' resetting their path integration system might be higher if they see a more stable visual item (e.g., a tree or a building). Future studies are required to investigate whether the retrieval process is still essential for people to use a more stable landmark to reset their positions in the path integration system. Note that the paths participants walked in the current project were relatively short. However, in large-scale environments, people cannot view the whole environment from a small number of viewpoints, and they need considerable locomotion to apprehend the whole environment (Montello, 1993). Whether our findings of the current study can be applied to this situation requires further investigations.

We also acknowledge that we did not measure how long participants looked at the landmark in each condition especially in Experiment 1. In Experiment 1, the landmark in the conflictATwalking condition was presented during participants' walking the second leg. The landmark in the conflictAFTERwalking condition was presented during participants' pointing to five targets. Therefore, the presence of the landmark was shorter in the former condition than in the latter condition. The eye fixation duration on the landmark, however, might not be shorter in the conflictATwalking condition than in the conflictAFTERwalking condition. Participants in the conflictATwalking condition should have looked at the landmark to guide their walking, as they needed to walk toward the landmark (instead of the green pole). In contrast, participants in the conflictAFTERwalking condition were only instructed to look at the landmark around their feet when they reached the green pole. Without any eye movement data, we could not precisely contrast the eye fixation duration on the landmark between conditions. Therefore, we could not determine whether or not the duration of the landmark presence played a role in generating the differences between these two conditions. Experiment 2 eased this concern. Participants in the 3-leg inconsistent pointing condition only pointed to one target in the presence of the landmark, but their path integration system was still reset. It seems that pointing to one target or five targets might not be critical for resetting. Instead, retrieval might be more critical than the presence of landmarks for resetting.

In summary, the current project demonstrated that participants relied on idiothetic cues rather than a displaced landmark in determining their positions when they did not judge their locations in the presence of the landmark. They switched to the displaced landmark in determining their positions when they judged their locations in the presence of the displaced landmark, and they used the position corrected by the visual landmark as the initial position of a new movement. These results indicate that the path integration system works dynamically during navigation, and the piloting system resets the path integration system intermittently, in particular when people are asked to retrieve the conflicting position representations produced by both systems.

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Appendix

The Proof of $OP' = \alpha - \alpha' + OP$ and $H' = \alpha - \alpha' - \beta + H$ (Mou & Zhang, 2014)

As illustrated in Figure 1 in the article, a hypothetical participant walks a 2-leg path, starting from O, turning at T, and ending at P (test position). The participant's test heading is H. The participant thinks they are standing at P′ and facing H′ during testing. The participant's response position of X is X′ and the response position of O is O′.

The participant thinks that they are standing at P′, when they are required to point to O and X, although the participant is actually standing at P and actually points to O′ and X′, respectively. The spatial relations among P, O′, and X′ should reflect the mental representations of the spatial relations among P′, O, and X. Therefore, the configuration formed by P, O′, and X′ is the same as the configuration formed by P′, O, and X regardless of the scale.

Mathematically speaking, the triangle P′OX is similar to the triangle PO′X′:

$$\Delta P'OX \sim \Delta\, PO'X'. \tag{1}$$

Next, we will have the bearing computations. We define a bearing as a signed angular distance from a reference direction in a horizontal plane. Mathematically, a reference direction can be any direction in the horizontal plane. For simplicity, here we use the direction from O to T as the reference direction. Therefore, the bearing of OT is 0°. We further define clockwise angular distances from the direction of OT as positive bearings. For example, the bearing of OP′ is 70°, if we suppose that the bearing of OP′ is 70° clockwise from the bearing of OT. As a bearing is a signed distance, we can apply addition and subtraction to bearings just as to real numbers. For example, the bearing of OP′ minus the bearing of OT is 70°; the bearing of OT minus the bearing of OP′ is −70°. We can also apply all rules in real number addition and subtraction to bearings. For example, because of the commutative law of addition, the bearing of OP′ add the bearing of OT is the same as the bearing of OT add the bearing of OP′ (i.e., 70°).

For simplicity, in the following computations, the bearing of AB is written as AB. For example, OP′ refers to the bearing of OP′. Therefore, addition (i.e., +) and subtraction (i.e., −) are between bearings. For example, P′O – OX refers to the bearing of P′O minus the bearing of OX. We also note that the difference of two opposite bearings (AB and BA) is 180° (AB – BA = 180°).

From Equation 1, we know that the angular distance from OX to OP′ (written as OP′ – OX) equals the angular distance from O′X′ to O′P (written as O′P – O′X′). Therefore,

$$OP' - OX = O'P - O'X'. \tag{2}$$

Because $OP' = P'O + 180°$ and $O'P = PO' + 180°$, we can change Equation 2 to

$$P'O - OX = PO' - O'X'. \tag{3}$$

As $-OX + OX = 0$, we can also have

$$P'O - PO = P'O - OX + OX - PO. \tag{4}$$

(*Appendix continues*)

Replacing $P'O - OX$ in Equation 4 with $PO' - O'X'$ according to Equation 3, we get

$$P'O - PO = PO' - O'X' + OX - PO$$
$$= (OX - PO) - (O'X' - PO'). \quad (5)$$

We refer to $OX - PO$ as α and to $O'X' - PO'$ as α'. Hence,

$$P'O - PO = \alpha - \alpha'. \quad (6)$$

Because $P'O = OP' + 180°$ and $PO = OP + 180°$,

$$P'O - PO = OP' - OP. \quad (7)$$

Replacing $P'O - PO$ in Equation 6 with $OP' - OP$ according to Equation 7, we have $OP' - OP = \alpha - \alpha'$. Therefore,

$$OP' = \alpha - \alpha' + OP. \quad (8)$$

As illustrated in Figure 1, the participant thinks that they are standing at P′, facing H′ when they are required to point to O, although the participant is actually standing at P, facing H and actually points to O′. The spatial relations between PO′ and H should reflect the mental representation of the spatial relations between P′O and H′. Because H and H′ are also signed angular distances from the bearing of OT, they can be added to or subtracted from any bearings and headings.

Therefore, we get the following equation:

$$PO' - H = P'O - H'. \quad (9)$$

Hence,

$$H' - H = P'O - PO' = P'O - PO + PO - PO'. \quad (10)$$

According to Equation 6, $P'O - PO = \alpha - \alpha'$. We also term $\beta = PO' - PO$. We get

$$H' - H = \alpha - \alpha' - \beta. \quad (11)$$

Therefore, we have

$$H' = \alpha - \alpha' - \beta + H. \quad (12)$$

In summary, we get $OP' = \alpha - \alpha' + OP$ (Equation 8) and $H' = \alpha - \alpha' - \beta + H$ (Equation 12).

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