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Dissociating position and heading estimations: Rotated visual orientation cues perceived after walking reset headings but not positions

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ABSTRACT

This project examined the roles of idiothetic cues due to individuals' movement and allothetic cues independent of individuals' movement in individuals' estimations of their position and heading during locomotion. In an immersive virtual environment, participants learned the locations of five objects and then moved along two legs of a path before positioning the origin and the objects. Participants' estimations of their test position and their test heading were calculated based on the responded objects' locations, using a method of dissociating position estimation and heading estimation developed in this project. Results showed that when a conflicting visual orientation cue was presented after walking, participants relied on the allothetic cues (i.e., the visual orientation cue) for their heading estimation, but on idiothetic cues for their position estimation. These results indicate that after participants updated their position in terms the origin of the path (homing vector) via path integration, they estimated their heading. These results are inconsistent with the theoretical models stipulating that homing vectors are specified in terms of participants' body coordinate systems, but are consistent with the models stipulating that both homing vectors and participants' heading are specified in terms of a fixed reference direction in the environment.

1. Introduction

The estimation of one's position and heading in an environment is critical to each locomotor. As locomotors move through the environment, they need to continuously determine (i.e., update) their position and heading to return to the nest or move to forage sites. The question of how locomotors return to the nest or move to forage sites in a straight line (i.e., path integration) has been the focus of substantial empirical and theoretical research within the domains of comparative cognition, developmental psychology, cognitive psychology, and neuroscience.

To understand how locomotors update their position and heading (facing direction), scientists need to separately measure their position estimation and heading estimation while they are moving. The place cells and head direction cells, which were discovered in rodents, provide a great tool to measure rodents' estimations of position and heading and, thus, to study how rodents update their position and heading. Consequently, huge advancements have been made in understanding rodents' spatial memory and navigation (Jeffery, 2007; Muller, Ranck, & Taube, 1996; Taube, 2007). For example, it is observed that rodents' place cells are sensitive to the boundaries of the environments (O'keefe and Burgess, 1996) whereas

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rodents' head direction cells are determined by a distal landmark (Taube, 2007). A variety of theoretical and computational models of rodents' spatial memory and navigation have been developed based on these empirical findings (Barry & Burgess, 2014; Poucet et al., 2014). However, no such a tool is available to separately measure the estimations of position and heading in humans. The lack of this tool has impeded the empirical investigation on how humans use different cues to estimate their position and heading during navigation and therefore has restricted the theoretical advancement in understanding human spatial navigation. The current project introduced a behavioral method to separately measure human participants' estimations of their position and heading. Using this method, this project investigated how human participants use idiothetic cues and allothetic cues to estimate their position and heading, and then differentiated between two theoretical models on the reference directions that humans use in path integration.

Path integration is a process in which individuals update their position and heading using movement information, such as travel directions and speeds (Etienne & Jeffery, 2004; Loomis, Klatzky, Golledge, & Philbeck, 1999). Here, all cues generated by self-movement (vestibular cues, proprioceptive cues, optic flows, and efferent copies of motor commands) are referred to as idiothetic cues (Whishaw & Brooks, 1999). By contrast, the external cues (e.g., visual), which can specify participants' locations and headings but do not depend on participants' movement, are referred to as allothetic cues (Whishaw & Brooks, 1999).

There are two different possible theoretical models regarding the reference direction that people use to update the vector between their current position and the origin of the walking path (homing vector) (Loomis et al., 1999). The first model is inspired by the ideas stipulating that individuals update the homing vector in terms of their body coordinate systems (Benhamou, Sauve, & Bovet, 1990; Fujita, Loomis, Klatzky, & Golledge, 1990; Wang & Spelke, 2002). At any step of movement, individuals record their body rotation or/and their body translation using the idiothetic cues such that they can calculate the transformation matrix between the body coordinate systems before and after moving. Multiplying the homing vector in terms of the body coordinate system before moving and the transformation matrix, individuals can compute the homing vector in the body coordinate system after moving. We refer to this model as the egocentric homing vector model. The second model is based on the idea that individuals update the homing vector in terms of some fixed reference direction in the environment (Gallistel, 1990; Gallistel & Matzel, 2013; Müller & Wehner, 1988; Zhang, Mou, & McNamara, 2011). At any step of movement, individuals record their travel vector in terms of the same fixed reference direction. By adding the homing vector before moving and the current moving vector, individuals can compute the new homing vector in terms of the fixed reference direction after moving. We refer to this model as the allocentric homing vector model. In the current project, we did not distinguish between Cartesian and polar coordinate systems that could be applied in both models (Vickerstaff & Cheung, 2010).

Both models are mathematically feasible. However, there is no direct evidence to differentiate between these two models in human path integration. In the current project, we did not claim that these two models should be differentiated by whether path integration uses idiothetic cues or allothetic cues. In particular, we did not take the position that the egocentric homing vector model uses only idiothetic information whereas the allothetic homing vector model uses allothetic cues as well as idiothetic information. According to this position, the egocentric homing vector model is a special case of the allocentric homing vector model. Hence, it is not surprising that the egocentric homing vector model, being a special case, provides a poorer fit.[1] Therefore, we did not differentiate between these two models with the use of idiothetic cues or allothetic cues. Indeed, we admitted that the allocentric homing vector model can be applied to the situations in which people only rely on the idiothetic cues during path integration. For example, without any allothetic cues, people might establish a fixed reference direction using their initial walking leg and then update their travel direction in terms of the fixed reference direction using the idiothetic cues (Mou, McNamara, & Zhang, 2013; Zhang et al., 2011).

Instead, we contrast these two models on the basis of their different implications regarding the relationship between individuals' estimation of their last travel direction and their estimation of their heading after walking. According to the allocentric homing vector model, individuals' estimated travel direction but not their estimated heading is critical to updating allocentric homing vectors during walking. When individuals indicate the location of the origin, they need to transfer the allocentric homing vector to the egocentric homing vector to execute their response egocentrically. To transfer the allocentric homing vector to the egocentric homing vector, individuals need to estimate their heading in terms of the allocentric reference direction. Therefore, individuals' estimation of their travel directions determines their position estimation or homing vectors during walking, whereas their headings need to be estimated when a response is egocentrically executed during the test. Hence individuals' estimated test heading might be reset during testing and differ from their estimated last travel direction. In contrast, according to the egocentric homing vector model, because homing vectors are always encoded in terms of individuals' body coordinate systems (i.e., their heading), they should be ready to indicate the home egocentrically (e.g., pointing to the origin) without estimating their heading in terms of any allocentric reference direction. Because individuals' heading is the same as the travel direction, the estimated test heading should be the same as the estimated last travel direction.

Therefore, the allocentric homing vector model predicts that individuals' estimated test heading and their estimated last travel direction can differ, whereas the egocentric homing vector model predicts that individuals' estimated test heading and their estimated last travel direction are the same. Because both models predict that individuals' estimated test position is determined by their

[1] We are grateful to an anonymous reviewer for this comment.

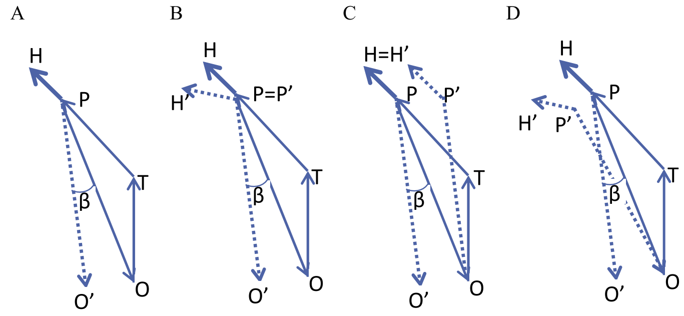

Fig. 1. Pointing errors (β) may be due to errors in the estimations of position, heading, or both. A hypothetical participant walks a two-leg path, starting from O (origin), turning at T (turning), and ending at P (test position). The participant's test heading is referred to as H. The participant points to O′ as the estimated position of O (A). The pointing error (β) is due to errors in the heading estimation. The participant's estimated test heading is referred to as H′. The estimated position is referred to P′. P = P′. β = H′–H (B). The pointing error (β) is due to errors in the position estimation. H = H′. β = P′O–PO (C). The pointing error (β) is due to errors in both heading and position estimations. H′ in terms of P′O equals H in terms of PO′ (D). Note that in the current project, addition (i.e., +) and subtraction (i.e., −) are between bearings rather than between vectors. For example, P′O–PO refers to the signed angular difference between P′O and PO rather than the vector subtraction of them.

estimated last travel direction, we can infer individuals' estimated last travel direction by using their estimated test position. Therefore, in the current project, to differentiate between these two models, we investigated whether the estimated test heading could be different from the estimated last travel direction by measuring individuals' estimated test heading and their estimated test position. Prior to the experimental description, we introduce the method of dissociating participants' position estimation and heading estimation.

One way to measure the accuracy of path integration is to point to the origin (e.g., Chance, Gaunet, Beall, & Loomis, 1998; Waller & Greenauer, 2007). However, the error in pointing to the origin cannot sufficiently dissociate the estimation of positions and the estimation of headings. As illustrated in Fig. 1A, a hypothetical participant walks two legs of a path, OT and TP, and then points to O while standing at P and facing H. The response direction is PO′. The measured pointing error is β. There are three possible interpretations of β. First, β might be due only to an inaccurate estimation of the heading (H′). As illustrated in Fig. 1B, the participant updates the position accurately, so the estimated position P′ is equal to the correct position P. However, the estimated heading (H′) is not accurate, such that β equals the difference between H and H′. Second, β might be attributed only to an inaccurate estimation of the position. As illustrated in Fig. 1C, the participant updates the heading accurately, so H′ equals H. However, P′ differs from P such that β equals the angular difference between OP′ and OP. Third, β might be attributed to inaccurate estimations of both the position and heading (as illustrated by Fig. 1D). β can be observed whenever the bearing of P′O in terms of H′ equals the bearing of PO′ in terms of H. Hence, in general, we cannot dissociate position estimation and heading estimation only using β.

In a study which is an exception, Klatzky, Loomis, Beall, Chance, and Golledge (1998) showed that the pointing error perfectly fit the turning angle between the first and second legs and concluded that the pointing errors might be attributed only to the heading estimation. However, the dissociation between participants' position estimation and their heading estimation would have been impossible if the pointing error did not equal the turning angle.

Homing (going back to the origin, e.g., Chrastil & Warren, 2013; Kearns, Warren, & Duchon, 2002; Riecke, van Veen, & Bulthoff, 2002) could dissociate the position error, measured as the distance between the stopping location and the origin; and the heading error, measured as the angular difference between the response turn of homing and the correct turn, in path integration. However in the current project, we were interested in participants' estimations of their position and their heading. Using the task of homing, we can only measure participants' estimation of their heading because participants' estimated position should be the origin, as they think they are back to the origin. For the interest of generality, we develop a method of dissociating individuals' position estimation and heading estimation when they are at places other than the origin.

In this method, individuals learn one more location in addition to the origin of a path before walking the path of two legs. In particular, they learn two objects placed at these two locations. After walking the two legs, individuals then place the objects back at their original locations by indicating the exact locations using a stick. As shown in Fig. 2A, an object X is placed around the origin, in which object O is placed. After individuals walk the two legs of the path, OT and TP, they indicate the exact locations of both O and X using a pointer stick while standing at P, facing H. Suppose individuals indicate O′ and X′ as the estimations of O and X, respectively. All the bearings in Fig. 2A are defined relative to the direction of OT. For example, OX indicates the direction of OX in terms of OT. We need to calculate the estimated test position and the estimated test heading, P′ and H′ respectively, in Fig. 2A.

This method is based on three assumptions.[2]

Assumption 1. Individuals accurately perceive and represent the direction of X in terms of their learning position and heading. In other words, the bearing of OX in terms of OT is

[2] We are grateful to an anonymous reviewer for the suggestions about the assumptions.

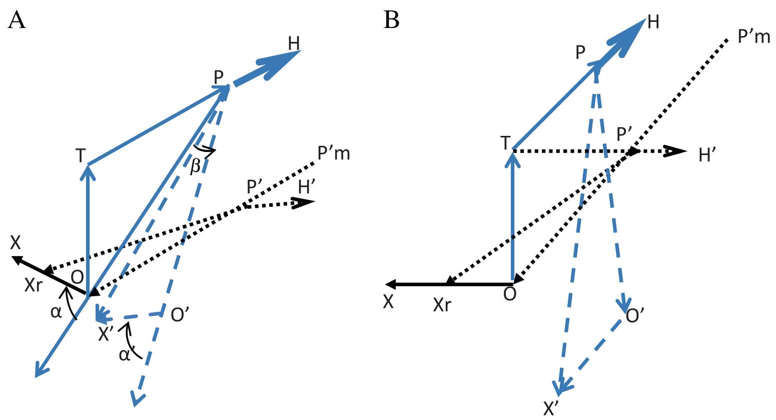

Fig. 2. (A) Dissociating heading assessment and position assessment using the estimated locations of the object in the origin (O) and of another object (X). A hypothetical participant walks a two-leg path, starting from O (origin), turning at T (turning), and ending at P (test position). The participant's test heading is referred to as H. The estimated position of O is O′. The represented position of X during learning is Xr. The estimated position of Xr is X′. The estimated test position is P′ and the estimated test heading is H′. P′m is the measured P′. β = PO′–PO. α = OX–PO. α′ = O′X′–PO′. (B) Illustrating that the triangle P′OXr is similar to the triangle PO′X′; the angle of PO′X′ is identical to the angle of P′OXr (P′OX).

accurately represented during learning. Because previous studies indicated that distance perception in virtual environments is underestimated (Thompson et al., 2004) and virtual environments was used in the current project, this assumption does not require that participants accurately perceive or represent the length of OX. Accordingly, we refer to the represented X during learning as Xr (see Fig. 2). The bearings of OX and OXr are the same whereas the length of OXr is shorter than the length of OX.

Assumption 2. Although individuals might be inaccurate in the path integration, that is P′ and H′ might not be the same as P and H, participants accurately update the directions and the distances of objects in terms of their estimated position (P′) and heading (H′). In particular, the bearings of P′Xr and P′O in terms of H′ are accurate and the lengths of P′Xr and P′O are also accurate.

Assumption 3. Individuals correctly execute their responses, indicating the directions of the updated object locations. In particular, the bearings of PX′ and PO′ in terms of H are the same as the bearings of P′Xr and P′O in terms of H′ respectively. Individuals might overshoot the lengths of PX′ and PO′ because the length of the virtual stick might be underestimated (Thompson et al., 2004). However, the ratio of the length of PO′ to the length of P′O equals the ratio of the length of PX′ to the length of P′Xr.

All these three assumptions are supported by the studies in the literatures of spatial updating showing that people can accurately point to objects visually perceived after walking a path (e.g. Siegle, Campos, Mohler, Loomis, & Bülthoff, 2009). Based on these three assumptions, the triangle P′OXr is similar to the triangle PO′X′, thus the angle of P′OX (i.e. P′OXr) equals the angle of PO′X′. We elaborate this idea using a concrete example. As illustrated in Fig. 2B, individuals learn the location of X, which is 1 m west of their body (O). According to Assumption 1, the bearing of X, but not the distance of X was accurately represented. Suppose the represented X (i.e. Xr) is 0.5 west of O due to perceptual or memory errors. Individuals then walk 1 m north, turn right 45°, and walk another 1 m. Finally they stop at P while facing H. Suppose individuals think they turned 90° instead of 45° but accurately estimate the travel distance. Therefore individuals think they stop at P′ while facing H′, as illustrated in Fig. 2B. According to Assumption 2, relative to their estimated position (i.e. P′), O is located 1.41 m away in the direction of 135° clockwise in terms of the estimated heading (P′O–H′ = 135°) and Xr is located 1.80 m away in the direction of 146° clockwise in terms of the estimated heading (P′Xr–H′ = 146°). According to Assumption 3, individuals execute their responses accurately in terms of directions but overshoot distances. Suppose individuals overshoot distances with a scale of 1.5. Therefore, relative to their physical location (P) and physical heading (H), O′ is located 2.12 m ($1.41 * 1.5$) away in the direction of 135° clockwise (PO′–H = 135°) and X′ is 2.7 m ($1.8 * 1.5$) away in the direction of 146° clockwise (PX′–H = 146°). As a result, the angle of OP′Xr equals the angle of O′PX′. Both angles are 11° (i.e., 146–135°). In addition, the ratio of the distance of PO′ to the distance of P′O equals the ratio of the distance of PX′ to the distance of P′Xr (both ratios are 1.5 in particular). Therefore, the triangle P′OXr is similar to the triangle PO′X′. Hence the angle of P′OX (i.e. P′OXr) equals the angle of PO′X′.

Because the angle of P′OX equals the angle of PO′X′, we get:

$$P'O - OX = PO' - O'X' \quad (1)$$

(Appendix for the equivalent equations in terms of angles for the readers who are more familiar with calculations in angles than in bearings).

Note that in the current project, addition (i.e., +) and subtraction (i.e., $-$) are between bearings rather than between vectors. For example, P′O–OX refers to the signed angular difference between P′O and OX rather than the vector subtraction of them.

As we use X rather than Xr to measure P′, the measured P′ (referred to as P′m in Fig. 2) is different from P′ when Xr is different from X (see Fig. 2). As proven above, the triangle P′OXr is similar to the triangle PO′X′. Because Xr is any given point between O and X including X but excluding O, the triangle P′mOX, as a special case of P′OXr, is also similar to the triangle PO′X′. Therefore, P′mOX is similar to P′OXr when X is different Xr. As X′ is on the ray starting at O and passing through Xr, P′m is on the ray starting at O and passing through P′. Hence, the bearing of OP′m is the same as the bearing of OP′, independent of the inaccuracy of encoding the distance of XO whereas the length of OP′m depends on the inaccuracy of encoding the distance of XO. The ratio of the length of OXr to the length of OX equals the ratio of the length of OP′ to the length of OP′m. In the example illustrated by Fig. 2B, the length of OP′m is twice the length of OP′ because the length of OX is twice the length of OXr. Consequently, the bearing of OP′m is the same as the bearing of OP′ whereas the position P′m is different from the position P′ whenever X is different from Xr. Because encoding of the distance of XO might be inaccurate as objects of X and O were presented in virtual environments in the current project (Thompson et al., 2004), we measure the bearing of OP′, which is the same OP′m, rather than the position P′, which might be different from P′m.

$$P'O - PO = P'O - OX + OX - PO \tag{2}$$

Replacing P′O–OX in Eq. (2) with PO′–O′X′ according to Eq. (1), we get:

$$\begin{aligned} P'O - PO &= PO' - O'X' + OX - PO \\ &= (OX - PO) - (O'X' - PO') \end{aligned} \tag{3}$$

OX–PO is determined given the locations of O, X, and P. O′X′–PO′ can also be determined from participants' responses to O, X (i.e., O′ and X′). Hence, the angular error in the position estimation (i.e., P′O–PO) can be calculated. P′O, the angular direction from the estimated test position to the origin (P′O) and vice versa (i.e., OP′), can also be calculated.

We refer to OX–PO in Eq. (3) as α and to O′X′–PO′ as α' (see Fig. 2A). The signed angular error of estimating the test position (i.e., P′O–PO) can be indicated by α–α'. Hence,

$$P'O - PO = \alpha - \alpha' \tag{4}$$

Because participants place the object back at the location of O′ while standing at P and facing H when they think they are placing the object back at the location of O while standing at P′ and facing H′, we get the following formula:

$$PO' - H = P'O - H' \tag{5}$$

In the example illustrated in Fig. 2B, PO′–H = P′O–H′ = 135°.

Hence,

$$H' - H = P'O - PO' = P'O - PO + PO - PO' \tag{6}$$

As P′O–PO = α–α', PO′–PO = β, we get

$$H' - H = \alpha - \alpha' - \beta \tag{7}$$

Hence, the angular errors in the heading estimation can be calculated. Accordingly, the estimated heading H′ can also be calculated.

As illustrated, if participants replace one object in addition to the object located at the origin, we can calculate the angular direction of the estimated position (OP′) and the estimated heading (H′) as well as the angular errors in the position estimation (OP′–OP) and in the heading estimation (H′–H). All the calculations depend on measurements of α' and β. In addition to the directions of PO′ and PX′ in terms of H, this method also uses the ratio of the distance of PO′ to the distance of PX′ to measure α' (see Fig. 2).

Random errors occur when participants learn the direction of X in terms of the learning position and heading (see the Assumption 1), when individual update the directions of X and O in terms of the estimated position (P′) and heading (H′) after walking the path (see the Assumption 2), and when they execute the responses indicating the direction of X and O in terms of the estimated position and heading (see the Assumption 3). All these random errors contribute to the random errors in measuring α' and β, thus also contribute to the random errors in measuring OP′ (see Eq. (4)) and H′ (see Eq. (7)). In the current project, participants learned four objects (X1, X2, X3, and X4) forming a square around their learning position and replaced these four objects in addition to the origin after traveling a path. Therefore, four pairs OP′ and H′ were calculated using the method described above and then the mean OP′ and H′ were calculated. The random errors in the mean OP′ and H′ due to the random error in measuring α' could be significantly reduced (the standard deviation of the random error in the mean OP′ and H′ could be reduced 50%). Although participants need to update five objects, they should still be able to update them as the previous studies showed that people can perform spatial updating of up to 5 locations as well as they can update a single location (Rieser & Rider, 1991). Furthermore, in the current project, participants were allowed enough time to learn the directions of five objects accurately (see details in Experiment 1 for the evidence). When participants replaced the objects, they used a visible virtual stick to indicate the positions without any time pressure to ensure that they executed their response as accurately as possible.

Some response errors might not be random. Participants might bias their responses about the objects' locations to the center of the object array (e.g. Haun, Allen, & Wedell, 2005; Huttenlocher, Hedges, & Duncan, 1991).[3] In the current project, the four objects other than the object at the origin formed a square such that the center of the square is exactly the origin. Therefore, if there was a response bias that causes the estimated position closer to the center, the estimated X′ might have been shifted to O′. The effect of this response bias is equivalent to the effect of encoding X closer to O. Consequently, the measured X′ might have been closer to O′ than the exact X′ should be. However this response bias does not change α' or β (Fig. 2). According to Eqs. (4) and (7), the measurements of OP′ and H′ are not affected by this response bias.

[3] We are grateful to an anonymous reviewer for this suggestion.

2. Experiment 1

Experiment 1 was designed to test the allocentric homing vector model and the egocentric homing vector model. In an immersive virtual environment (see Fig. 3), participants learned one object located at the learning position and four objects around the learning position inside a large circular wall. The wall had 12 numbers (1, 2, 3, ..., and 12) presented in order and with an angular step of 30°. We referred to the wall as clockwall below. The size of the clockwall was very large, such that it only provided good information about participants' rotation but not their translation (In Fig. 3, the clockwall was drawn at a scale of 0.06 to fit the figure.) Participants physically walked paths (i.e., O–T–P) and then at the end of the path (i.e., P), placed each object back at its original location using a virtual stick. The clockwall and the objects disappeared when participants started to walk the first leg (i.e., OT). The clockwall with a rotation of 100° in the direction opposite participants' turning direction (Fig. 3B) reappeared either while participants were walking the second leg (i.e., TP, and disappeared during test; see the *RotatedClockwall during 2nd leg* in Table 1) or after they walked the second leg (i.e., TP, and remained present during the test; see the *RotatedClockwall during test* in Table 1), indicating an orientation different from the one suggested by idiothetic cues.

In the conditions of the *RotatedClockwall during 2nd leg* (see Table 1), participants relied on the conflicting allothetic cue (i.e., the rotated clockwall) and idiothetic cues to determine their last travel directions. Because there was no additional information presented during testing, participants had to use the estimated last travel direction as their estimated heading during the test. Therefore both models predict that participants' estimated test heading should be the same as the estimated last travel direction.

In the conditions of the *RotatedClockwall during test* (see Table 1), however, these two models lead to dissociable predictions. In these conditions, only the idiothetic cues determine the last travel direction because the rotated clockwall was not present during walking. Nevertheless, the conflicting idiothetic cues and the allothetic cue (the rotated clockwall) were both available during the test. According to the allocentric homing vector model, individuals need to estimate their heading during the test to respond egocentrically. Participants had to weight the conflicting allothetic cues and idiothetic cues to estimate their test heading. We assume that the allothetic cues may be more reliable than the idiothetic cues to determine the heading during the test because idiothetic cues may be important during locomotion but may not be important after locomotion. Consequently, as the rotated clockwall determines the estimated test heading, the estimated test heading differs from the estimated last travel direction. In contrast, the egocentric homing vector model stipulates that individuals update the homing vector in terms of their body coordinate systems (i.e., their heading). When participants indicate the home, they do not need to estimate their heading relative to any allocentric reference direction. Therefore, the estimated test heading should be the same as the estimated last travel direction.

We also investigated whether the reliability of cues affects the relative importance of cues in position estimations and heading estimations (Etienne & Jeffery, 2004; Foo, Warren, Duchon, & Tarr, 2005). In Experiment 1, half of the participants directly turned to the direction of the second leg (turning-only conditions in Table 2), whereas the other half rotated two circles (i.e. 720°) before turning to the direction of the second leg (rotation plus turning conditions in Table 2). We expected that the rotation would reduce or eliminate the reliability of idiothetic cues.

More specifically, participants learned objects' locations with the presence of the clockwall (Fig. 3A). Then they physically walked two-leg paths (O–T–P) that included a 50° turn to the right or left. During the first leg (i.e., OT), the clockwall disappeared. The clockwall appeared again with a rotation of 100° in the direction opposite participants' turning direction only during either the second leg (TP) or the test phase (Fig. 3B). At the turning point (T in Fig. 3), participants directly turned 50° to face the direction of the second leg (or the green pole, P, in Fig. 3) or rotated 720° before they turned to face the direction of the second leg. Thus, four conditions were created according to the combinations of the onset of the rotated clockwall and whether participants rotated 720° before they turned to face the direction of the second leg (see Table 1).

A B

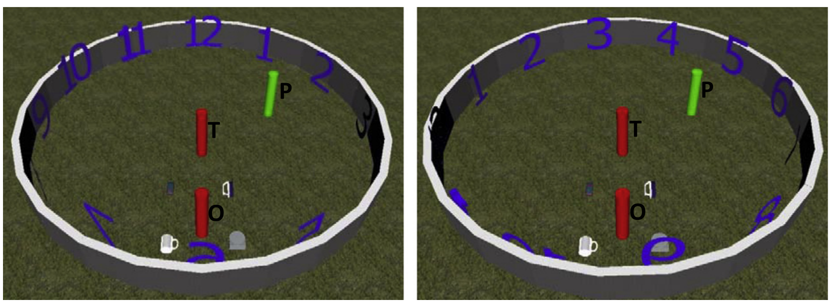

Fig. 3. Schematic diagram of the experiment setup (bird's eye view) for Experiment 1. The clockwall was drawn at a scale of 0.06 to fit the figure. All the objects, the clockwall, and the poles were presented together only for readers. Participants learned the objects' locations while facing the number 12 on the clockwall (A). The clockwall disappeared when participants started to walk OT but appeared again with a rotation of 100° in the opposite direction of participants' turning direction during the time when participants walked TP or after participants had walked TP (B).

Table 1
Cue conditions in Experiment 1.

	RotatedClockwall during 2nd leg	*RotatedClockwall during test*
Turning only	*T_RotatedClockwallAT2ndleg*	*T_RotatedClockwallATtesting*
Rotation plus turning	*R+T_RotatedClockwallAT2ndleg*	*R+T_RotatedClockwallATtesting*

Table 2
Predictions of the position and heading estimations based on the two different theories, and the angular means (mean lengths) of the observed position and heading in different cue conditions in Experiment 1.

	Prediction from egocentric homing theory		Prediction from allocentric homing theory		Observed circular mean (length of mean vector, *r*)	
	Position	Heading	Position	Heading	Position	Heading
T_RotatedClockwallAT2ndleg	25°	50°	25°	50°	26° (0.82)	57° (0.85)
R+T_RotatedClockwallAT2ndleg	75°	150°	75°	150°	64° (0.56)	129° (0.66)
T_RotatedClockwallATtesting	25°	50°	25°	150°	24° (0.67)	147° (0.65)
R+T_RotatedClockwallATtesting	Random	Random	Random	150°	Random	148° (0.95)

Because the lengths of the first leg and the second leg were the same (lengths of OT and TP were both 1.8 m), the direction of OP, in terms of the direction of OT, should be half of the turning angle (i.e., TP in terms of the direction of OT, see Fig. 2). Further, the heading (H), should be the same as the turning angle (i.e., TP in terms of the direction of OT, see Fig. 2). Similarly, the direction of OP′, in terms of the direction of OT, would be the half of the turning angle that participants estimated using the idiothetic cues or the visual cues. The heading H′, in terms of the direction of OT, would be the same as the turning angle which participants estimated using the idiothetic cues or the visual cues.

Both the egocentric homing vector theory and the allocentric homing vector theory predict that participants' estimated test headings would be the same as their estimated last travel direction under the conditions in which the rotated clockwall was presented during the second leg (see *RotatedClockwall During 2nd leg* in Table 1). In the turning-only condition (*T_RotatedClockwallAT2ndleg*), the estimations of the test position and the test heading would both be determined by the idiothetic cues (i.e., 50° turning angle) assuming idiothetic cues are dominating during locomotion. OP′ with respect to OT should be half of the estimated turning angle (i.e., approximately 25°). H′ with respect to OT should be the same as the estimated turning angle (i.e., approximately 50°). In the turning-after-rotation condition (*R+T_RotatedClockwallAT2ndleg*), the estimations of the test position and the test heading would both be determined by the allothetic cue (i.e., clockwall) that indicated a 150° turning angle because idiothetic cues were not reliable after the 720° rotation due to the rotation itself or due to the time for the rotation. With respect to OT, OP′ should be approximately 75°, i.e., half of the estimated turning angle; H′ should be approximately 150°, i.e., the same as the estimated turning angle.

In contrast, the egocentric homing vector model and the allocentric homing vector model have different predictions for the conditions of the rotated clockwall being presented during the test (see *RotatedClockwall during test* in Table 1). The egocentric homing vector theory still predicts that the estimated test heading was the same as the estimated last travel direction. According to this model, in the turning-only condition (*T_RotatedClockwallATtesting*), both estimations of the heading and the position would be determined by the idiothetic cues (i.e., a 50° turning angle). With respect to OT, OP′ should be approximately 25° and H′ should be approximately 50°. In the turning-after-rotation condition (*R+T_RotatedClockwallATtesting*), both estimations of the heading and the position would be random, as participants could not accurately estimate their turning angle after the 720° rotation. By contrast, based on the allocentric homing vector model, the estimated test heading could differ from the estimated last-travel direction and would be reset by the rotated clockwall during the test. According to this model, in the turning-only condition (*T_RotatedClockwallATtesting*), the estimation of the position would be determined by the idiothetic cue (i.e., the 50° turning angle), whereas the estimation of the heading would be determined by the rotated clockwall (i.e., the 150° turning angle). With respect to OT, OP′ should be approximately 25°, i.e., half of the turning angle indicated by the idiothetic cue; H′ should be approximately 150°, i.e., the same as the turning angle indicated by the clockwall. In the turning-after-rotation condition (*R+T_RotatedClockwallATtesting*), the estimation of the test position (OP′) would be random as participants could not accurately estimate their last travel direction, whereas the estimation of the test heading with respect to OT should be approximately 150°, i.e., the same as the heading indicated by the clockwall. These predictions are summarized in Table 2.

2.1. Method

2.1.1. Participants

Forty-eight university students (24 men and 24 women) participated in this experiment as partial fulfillment of a requirement for an introductory psychology course.

2.1.2. 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. Virginia). Head motion was tracked with an InterSense IS-900 motion tracking system (InterSense, Inc., Massachusetts). The virtual environment had a circular grass-textured ground with a radius of 10,000 m (Fig. 3A). The center of the virtual environment overlapped with the center of the physical room. A clockwall with a radius of 50 m and a height of 10 m was presented during learning and disappeared when participants started to walk. The clockwall's center was also the center of the physical room (see Fig. 3, the clockwall was drawn at a scale of 0.06 to fit the figure). The clockwall had a gray texture and had 12 numbers (1–12) evenly placed on it. The radius of the clockwall was too large to provide translation information. Participants held an InterSense IS-900 Wand (InterSense, Inc., Massachusetts). The wand controlled a virtual stick; participants could move the wand to indicate any position on the ground, analogous to using a mouse to move a cursor to indicate a position on a computer screen.

Each participant finished two paths. For both paths, the first and the second legs were 1.8 m. One path had a turning angle of 50° clockwise and the other had a turning angle of 50° counterclockwise. The turning position of the path (illustrated by T in Fig. 3) was always at the center of the physical room. Before walking a path, participants learned the locations of five objects (ball, brush, phone, mug, and clock). One object was located at the origin (O). The other four objects were located 1.41 m from O in the directions of 315°, 45°, 135°, and 225° clockwisely (referred to as X1, X2, X3, and X4 respectively) relative to the direction of OT. The associations between positions and objects were random across participants but consistent across the two paths of each participant.[4] For each path, the origin and the turning position (O, T) were indicated by a red pole, and the test position was indicated by a green pole (see Fig. 3). The poles were 1.5 m in height and 0.05 m in radius. The poles were presented as a sequence to guide participants to walk the path (Kelly, McNamara, Bodenheimer, Carr, & Rieser, 2008). The poles disappeared once participants arrived at their positions.

Four conditions were involved in this experiment (see Table 1): the *T_RotatedClockwallAT2ndleg* condition, in which the rotated clockwall was presented during the second leg (Fig. 4A) and participants turned to face the green pole directly after they finished the first leg; the *R+T_RotatedClockwallAT2ndleg* condition, in which the rotated clockwall was presented during the second leg (Fig. 4A) and participants rotated for two circles and then turned to face the green pole after they finished the first leg; the *T_RotatedClockwallATtesting* condition, in which the rotated clockwall was presented after participants finished the two legs (Fig. 4B) and participants turned to face the green pole directly after they walked the first leg; and the *R+T_RotatedClockwallATtesting* condition, in which the rotated clockwall was presented after participants finished the two legs (Fig. 4B) and participants rotated for two circles and then turned to face the green pole after they walked the first leg. Twelve participants (six men) were randomly assigned to each of the four conditions.

As discussed in the Introduction, estimated positions of the origin and one other object are sufficient to calculate the estimated test position and estimated test heading. Four objects other than the object at the origin, however, were used to increase the accuracy of calculation. Four pairs of estimated heading (H′) and estimated position vector (OP′) were calculated for each path and each participant. The mean of the four H′ and the mean of the four OP′ for each path and each participant were used in data analyses below.

2.1.3. Procedure

Before walking each path, participants were asked to look for the red pole and to walk toward it, which would be the origin of the path. After participants reached the pole, the pole disappeared. Participants were asked to search for another red pole (illustrated by T in Fig. 3) and to turn to face it. Then, the red pole disappeared.

In the study phase, participants saw the clockwall, and five objects appeared on the ground (Fig. 4); they faced the number 12 on the clockwall, and they were allowed to turn around to see all the numbers on the clockwall. Participants studied the five objects for 3 min for the first path and studied the objects for 30 s for the second path. Thirty seconds of learning for the second path was sufficient for participants to remember the locations as the locations of the objects were the same relative to participants' learning position and orientation (from O to T) in both paths. To ensure that participants would use the orientation indicated by the clockwall, participants were asked to close their eyes and the experimenter spun them for 15 s on the swivel chair after they learned the objects. Participants were then instructed to open their eyes and turn back to their original orientation by referring to the clockwall. All participants did this accurately. Afterwards, participants were asked to replace each object by pointing the virtual stick to the remembered position using the wand. Each object was probed in a random order. Feedback was given by showing the object in the correct location for five seconds. Then the participant replaced the next object. After participants replaced all the objects once, they replaced the objects a second time and were given feedback again. Then, the red pole in front of participants (illustrated by T in Fig. 3) appeared again and the clockwall disappeared (Fig. 4). Participants walked toward the red pole. When they arrived at the red pole, the red pole disappeared. The procedure was the same for all groups until participants finished the first leg (Fig. 4).

In the rotation plus turning conditions (i.e., *R+T_RotatedClockwallAT2ndleg* and *R+T_RotatedClockwallATtesting*), participants spun clockwise until the experimenter stopped them. Participants turned 360°. In a similar way, they turned 360° counterclockwise. After rotation, participants were asked to turn to face the green pole and then walk toward it. In contrast, in the turning-only conditions (i.e., *T_RotatedClockwallAT2ndleg* and *T_RotatedClockwallATtesting*), participants were asked to turn to face the green pole and walked toward it immediately after they walked the first leg.

[4] For example, for one participant the ball was placed in the direction of 225° (i.e. X4) relative to the direction of OT for both paths whereas for another participant the ball was placed in the direction of 45° (i.e. X2) relative to the direction of OT for both paths.

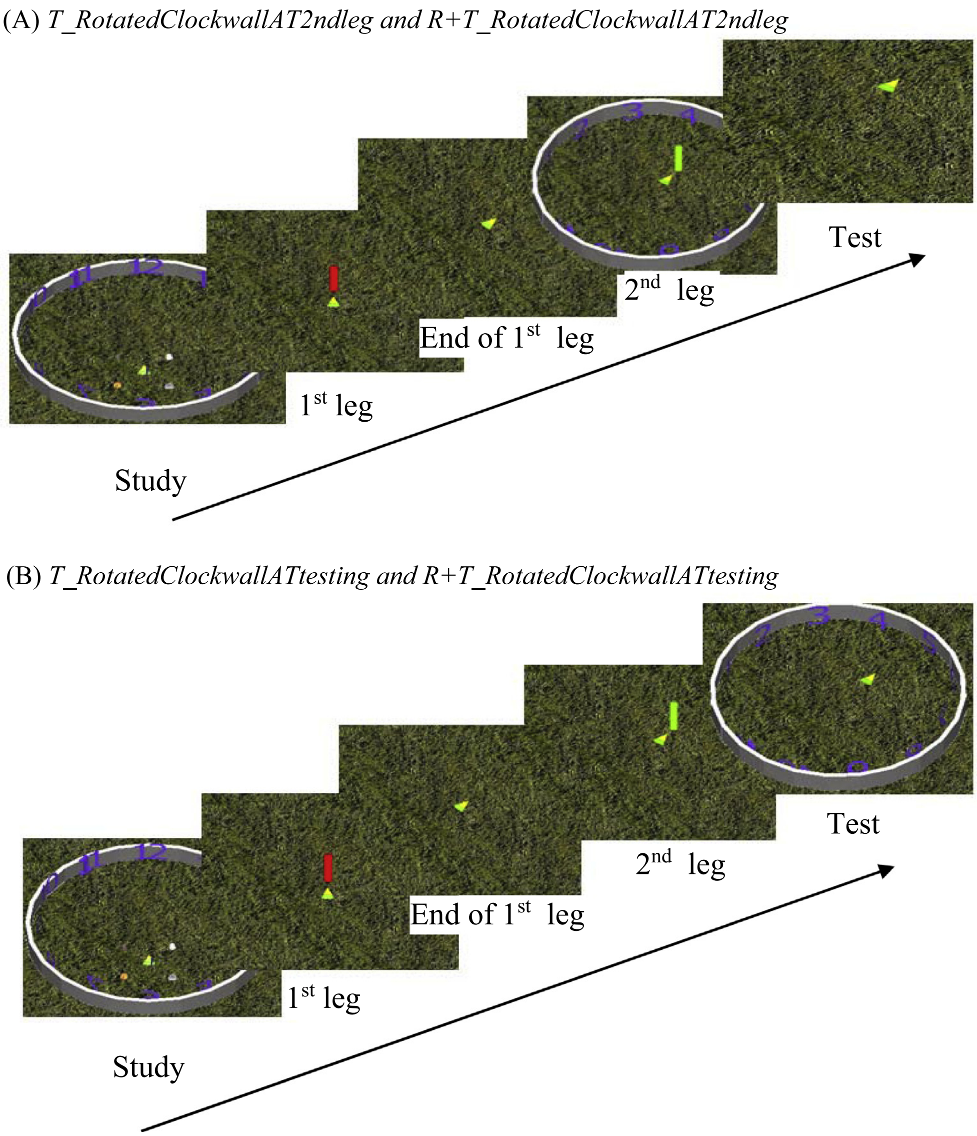

Fig. 4. Timeline of Experiment 1. Participants' physical standing position is denoted by a yellow–green triangle with the top yellow part indicating participants' heading. In the study phase, participants learned five objects' positions. In the locomotion, participants walked towards a red pole in the first leg and then a green pole in the second leg. (A) The conditions of *T_RotatedClockwallAT2ndleg* and *R+T_RotatedClockwallAT2ndleg*, (B) the conditions of *T_RotatedClockwallATtesting* and *R+T_RotatedClockwallATtesting*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Regarding the onset of the rotated clockwall, in the *Rotatedclockwall during second leg* conditions (*T_RotatedClockwallAT2ndleg* and *R+T_RotatedClockwallAT2ndleg*), the rotated clockwall appeared after participants faced the green pole and disappeared after participants reached the green pole (Fig. 4A). By contrast, in the *RotatedClockwall during test* conditions (*T_RotatedClockwallATtesting* and *R+T_ RotatedClockwallATtesting*), the rotated clockwall only appeared when participants reached the green pole (Fig. 4B).

During the test, participants replaced all objects once using the wand. Only one replaced object was visible at a time. Once replaced, the object was removed from the ground. No correct location was presented as a feedback.

2.1.4. Data analysis

To dissociate the allocentric homing vector theory from the egocentric homing vector theory (see the predictions in Table 2), we calculated the angular direction of the estimated test position, OP′, and the angular direction of the estimated test heading, H′, both relative to the first walking leg, OT. As the angular direction was circular data, Watson–Williams *F* tests were used to compare the directional difference among conditions. For each condition, the Rayleigh *Z* test was used to assess whether OP′ and H′ had uniform distributions, which would indicate a random estimation. The circular means of OP′ and H′ and their corresponding confidence intervals were also calculated. The confidence interval was used to test whether the mean OP′ and the mean H′ differed from their predicted directions based on the two theories (Batschelet, 1981). The parametric test for concentration examined differences in the estimation variability across the conditions (Batschelet, 1981, p. 122). The signs of OP′ and H′ for the path with the left turn were changed and combined with those for the path with the right turn, leading to 24 estimated test positions (two for each participant) and 24 estimated test headings (two for each participant) in each condition.

2.2. Results

2.2.1. Angular direction of the estimated test position, OP′

The OP′s in all conditions are plotted in Fig. 5. The mean OP′s and the lengths of the mean OP′s (r) are also listed in Table 2. The OP′s were clustered around 25° in the *T_RotatedClockwallAT2ndleg* condition (Fig. 5A), 75° in the *R+T_RotatedClockwallAT2ndleg* condition (Fig. 5B), and 25° in the *T_RotatedClockwallATtesting* condition (Fig. 5C) but were not clearly clustered in the *R+T_RotatedClockwallATtesting* condition (Fig. 5D).

As revealed by a Watson-Williams F test, the circular mean of the OP′s differed across conditions, $F(3,92) = 5.85$, $p = .001$. The Rayleigh Z test showed that the OP′s in the *R+T_RotatedClockwallATtesting* condition (Fig. 5D) were uniformly distributed ($Z = 1.31$, $p = .27$), whereas the OP′s in the other three conditions were clustered around one direction ($Zs \geqslant 7.47$, $ps < .001$). According to the confidence interval test, the circular mean of the OP′s in the *T_RotatedClockwallAT2ndleg* condition (Fig. 5A) was not significantly different from 25° ($p > .05$), but different from 75° ($p < .05$). The circular mean of the OP′s in the *R+T_RotatedClockwallAT2ndleg* condition (Fig. 5B) was not significantly different from 75° ($p > .05$), but different from 25° ($p < .05$); the circular mean of the OP′s in the *T_RotatedClockwallATtesting* condition (Fig. 5C) was not significantly different from 25° ($p > .05$), but different from 75° ($p < .05$).

The OP′s were more variable in the *R+T_RotatedClockwallAT2ndleg* condition than in the *T_RotatedClockwallAT2ndleg*

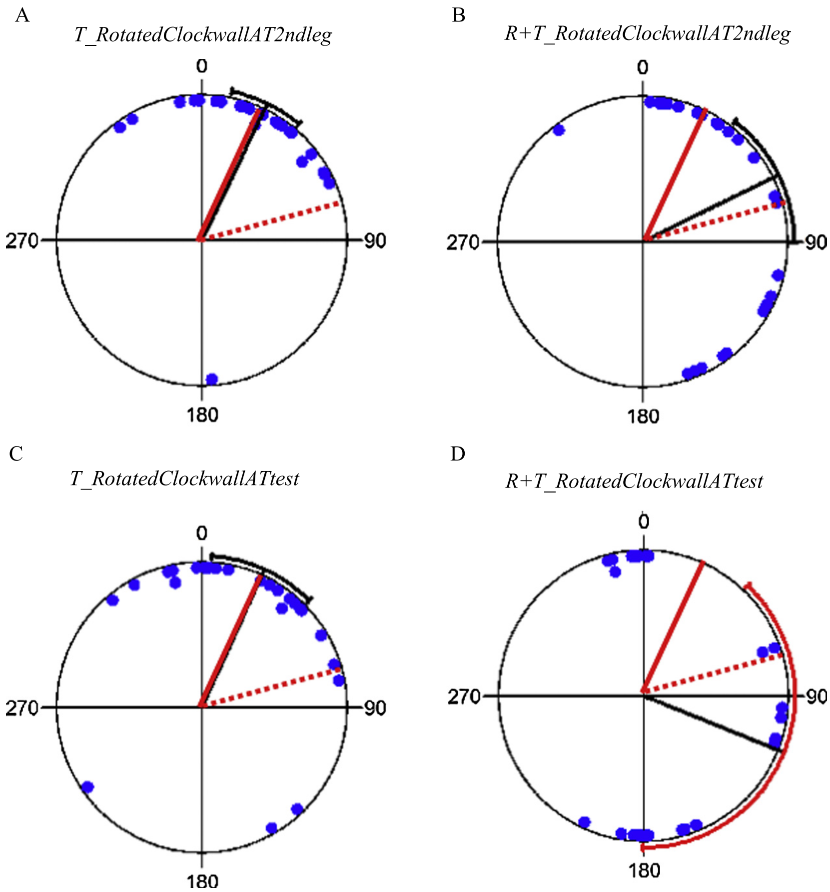

Fig. 5. Observed and predicted angular directions of the estimated test position (OP′) in the conditions of *T_RotatedClockwallAT2ndleg* (A), *R+T_RotatedClockwallAT2ndleg* (B), *T_RotatedClockwallATtesting* (C), and *R+T_RotatedClockwallATtesting* (D) in Experiment 1. Each blue dot indicates one individual observed OP′ (the signs of OP′ for the path with the left turn were changed). The black line indicates the mean 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 solid red line (25°) indicates the predicted direction of OP′ following the 50° turning angle indicated by the idiothetic cues. The dashed red line (75°) indicates the predicted direction of OP′ following the 150° turning angle indicated by the rotated clockwall. Note that in panels A and C, the black lines and the read lines overlap. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

condition, $F(23,23) = 2.47$, $p = .02$ (Batschelet, 1981, p. 122). The OP's were more variable in the *R+T_RotatedClockwallATtesting* condition than in the *T_RotatedClockwallATtesting* condition, $F(23,23) = 2.32$, $p = .02$ (Batschelet, 1981, p. 122).

2.2.2. Angular direction of the estimated test heading, H′

The H′s in all conditions are plotted in Fig. 6. The mean H′s and the length of the mean H′s (r) are also listed in Table 2. The H′s were clustered around 50° in the *T_RotatedClockwallAT2ndleg* condition (Fig. 6A) and around 150° in the other three conditions (Fig. 6B–D).

As revealed by the Watson–Williams F test, the circular mean of the H′s differed across conditions, $F(3,92) = 25.62$, $p < .001$. The Rayleigh Z test showed that the H′s in all conditions was clustered around one direction ($Zs \geqslant 10.23$, $ps < .001$). According to the confidence interval test, the circular mean of the H′s in the *T_RotatedClockwallAT2ndleg* condition (Fig. 6A) was not significantly different from 50° ($p > .05$), but different from 150° ($p < .05$). The circular mean of the H′s in each of the other three conditions (Fig. 6B–D) was not significantly different from 150° ($ps > .05$), but different from 50° ($ps < .05$).

The H′s were more variable in the *R+T_RotatedClockwallAT2ndleg* condition than in the *T_RotatedClockwallAT2ndleg* condition, $F(23,23) = 2.23$, $p = .03$ (Batschelet, 1981, p. 122). In contrast, the H′s were less variable in the *R+T_RotatedClockwallATtesting* condition than in the *T_RotatedClockwallATtesting* condition, $F(23,23) = 6.94$, $p < .001$ (Batschelet, 1981, p. 122).

The results, however, depend on the validation of the method of dissociating participants' position estimation and heading estimation. The validation of the method depends on the validation of the assumptions of the method. The assumptions require that participants learned the directions of the objects around the origin accurately, that participants updated the locations of the objects accurately, and that participants executed their responses accurately. To determine whether participants learned the directions of the objects around the origin accurately, we calculated the angular error, which is the angular difference between the bearing from the origin to the response

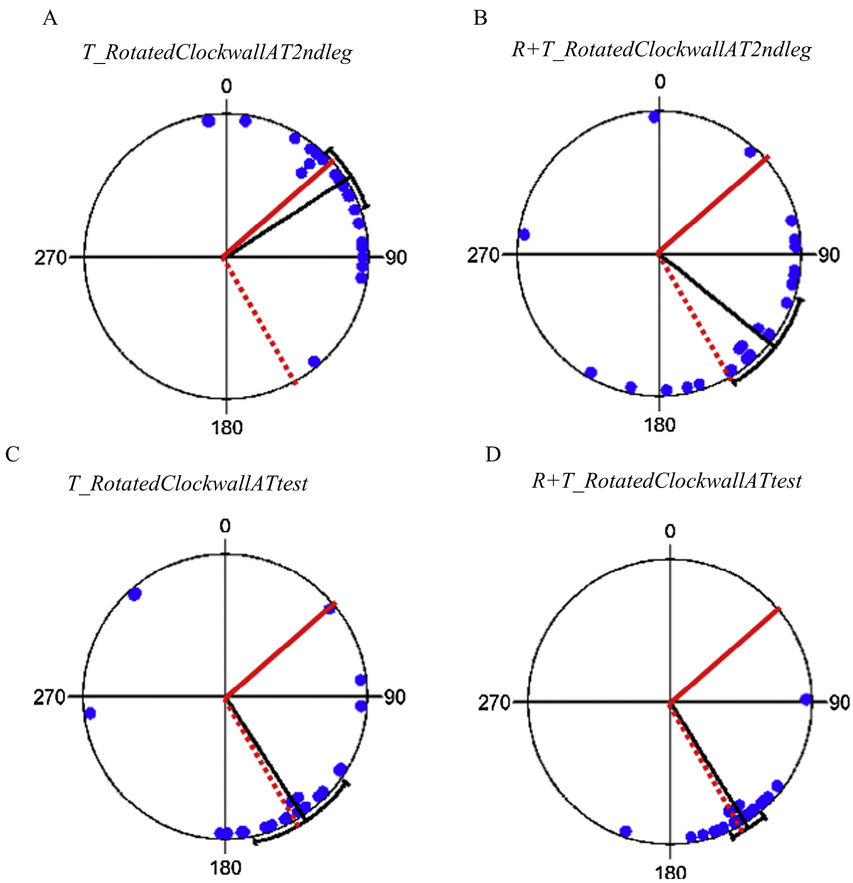

Fig. 6. Observed and predicted angular directions of the estimated test heading (H′) in the conditions of *T_RotatedClockwallAT2ndleg* (A), *R+T_RotatedClockwallAT2ndleg* (B), *T_RotatedClockwallATtesting* (C), and *R+T_RotatedClockwallATtesting* (D) in Experiment 1. The blue dots indicate individuals' observed H′s (the signs of H′ for the path with the left turn were changed). The black line indicates the mean direction 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 solid red line (50°) indicates the predicted direction of H′ following the 50° turning angle indicated by the idiothetic cues. The dashed red line (150°) indicates the predicted direction of H′ following the 150° turning angle indicated by the rotated clockwall. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

object's location and the bearing from the origin to the correct object's location, when participants replaced the objects locations for the second time while standing at the origin in the learning phrase for each path. The mean absolute angular error across paths, participants, and conditions was 7°, 10°, 11°, and 12° for X1, X2, X3, and X4 respectively indicating that participants learned the directions of the objects around the origin accurately. The circular mean of the angular error across paths, participants, and conditions was −5°, 8°, −5°, and 7° for X1, X2, X3, and X4 respectively, indicating that participants might represent objects' locations or point to objects' locations slightly away from their front–back body axis and toward their left–right body axis.

To determine whether participants updated the locations of the objects accurately and executed their responses accurately, we calculated angular distance between two adjacent vectors from the estimated origin to one estimated object position (i.e. O′X2′–O′X1′, O′X3′–O′X2′, O′X4′–O′X3′, O′X1′–O′X4′). If participants updated the locations of the objects accurately and executed their responses accurately, the angular distance should be close to 90° because the angular distance between two adjacent vectors from the origin to one object position (i.e. OX2–OX1, OX3–OX2, OX4–OX3, OX1–OX4) is 90°. The circular mean of the angular distance across paths, participants, and conditions was 96°, 79°, 94°, and 79° (the length of mean vector, r was .67, .74, .71, and .83) for O′X2′–O′X1′, O′X3′–O′X2′, O′X4′–O′X3′, O′X1′–O′X4′ respectively. The slight deviation from 90° for each angular difference can be explained by the speculation that participants represented objects' locations slightly away from their front–back body axis as shown by the mean signed angular errors in the learning phrase. Therefore, these results indicate that during locomotion, participants updated the locations of the objects accurately and executed their responses accurately.

2.3. Discussion

The results clearly fit the predictions of the allocentric homing vector model but do not fit the predictions of the egocentric homing vector model (see Table 2). As discussed in the introduction, we favor the allocentric homing vector model, because the estimated last travel direction was different from the estimated testing heading when the rotated clockwall was presented during the test (see the conditions of *T_RotatedClockwallATtesting* and *R+T_RotatedClockwallATtesting* in Table 2), rather than participants could use allothetic cues during locomotion. Indeed, participants in the *T_RotatedClockwallAT2ndleg* condition tended to ignore the allothetic cues (i.e., rotated clockwall) during locomotion, although they might still have updated the homing vector in terms of an allocentric reference direction (see a more detailed explanation in the general discussion).

This conclusion, however, depends on the validation of the method of dissociating participants' position estimation and heading estimation. Above, we did some post hoc analyses to support the assumptions of this method. To further validate the method, we validated it empirically in Experiment 2 without examining any assumptions. Furthermore, in Experiment 1, poles were presented to indicate the ending position of the next leg to guide participants to walk the paths in the virtual environments (Kelly et al., 2008). In particular, participants saw the pole placed at T when they started to walk the leg of O–T; participants saw the pole placed at P when they started to walk the leg of T–P (Fig. 3). The direction of P in terms of T should be perceived with the idiothetic cues as participants needed to turn their heads to find the location of the pole placed at P. However participants might have gained distance information about the next leg by seeing the next pole before they walked the leg. Hence some allothetic cues about travel distances were available even for participants in the *RotatedClockwallATtest* conditions. It is unlikely that participants, while standing at the testing position, could know the position of the origin only using the distance information provided by the poles presented as a sequence. However we still need to demonstrate that path integration for participants in *RotatedClockwallATtesting* conditions primarily relied on the idiothetic cues during walking.

3. Experiment 2

The primary purpose of Experiment 2 was to independently validate the method of dissociating the estimations of position and heading. The secondary purpose was to verify that participants in *RotatedClockwallATtesting* conditions of Experiment 1 primarily relied on the idiothetic cues in path integration.

The general idea of this experiment is based on the well-established finding that participants who actually walk a path can update their position and heading accurately whereas participants who primarily perceive optic flows of walking a path cannot (e.g. Chance et al., 1998; Chrastil & Warren, 2013; Kearns et al., 2002; Riecke et al., 2002; Ruddle, Volkova, Mohler, & Bulthoff, 2011; Waller & Greenauer, 2007). If the method of dissociating the estimations of position and heading is valid, the position error (P′O–PO in Eq. (4)) and the heading error (H′–H in Eq. (6)) should be smaller for individuals who physically walk than those who perceive optic flows. Therefore, in Experiment 2, we used the position error (P′O–PO) and the heading error (H′–H) to measure the inaccuracy in position estimation and heading estimation.[5]

More specifically, in four conditions, we factorially manipulated the cues that might be important to accurate position estimation and accurate heading estimation during locomotion (see Table 3). In the walking condition, participants physically walked paths (O–T–P) in an immersive virtual environment with a grassland texture on the ground (see Fig. 7A). The walking condition provided a

[5] In Experiment 1, position estimation (OP′) and heading estimation (H′) were the dependent variables because the egocentric homing vector model and the allocentric homing vector model could be dissociated by the relationship between the position estimation (OP′) and the heading estimation (H′). It is not clear how the egocentric homing vector model and the allocentric homing vector model can have any dissociable predictions in terms of position error or heading error.

Table 3
Locomotor conditions, available cues, and predictions of position estimation and heading estimation in each condition in Experiment 2.

	Cues available (study)	Cues available (locomotion)	Cues available (test)	Prediction of position estimation	Prediction of heading estimation
Walking	Grassland	Idiothetic, grassland	Grassland	Accurate	Accurate
Transportation	Grassland	Grassland	Grassland	Inaccurate	Inaccurate
Clockwall	Grassland	Grassland, clockwall	Grassland	Inaccurate or less accurate	Accurate
Disorientation	Grassland	Idiothetic, grassland, disoriented after walking	Grassland	Accurate	Chance level

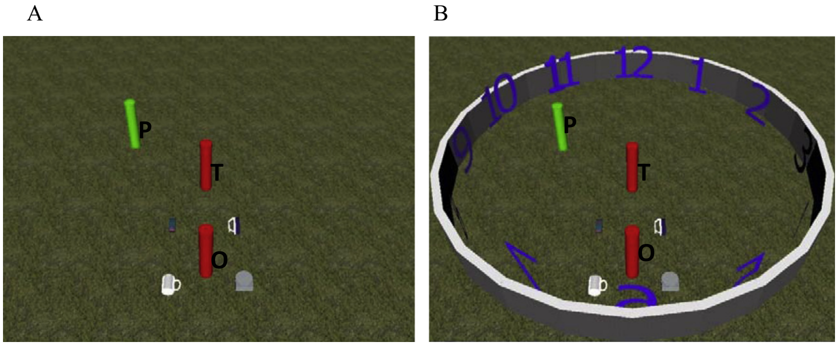

Fig. 7. Schematic diagram of the experimental setup (bird's eye view) for Experiment 2. Panel A indicates the conditions of walking, transportation, and disorientation. The object array indicates the locations of objects. The center object was located at the origin (O) of the path. The other four objects were located 1.41 m from the center object in the directions of 45°, 135°, 225°, and 315° with respect to the first walking path (OT). The lengths of OT and TP are both 1.8 m. The two red poles indicate the origin (O) and the turning point (T). The green pole indicates the test position (P). Panel B indicates the condition with the clockwall. The clockwall was 50 m in radius and 10 m in height. The clockwall was drawn at a scale of 0.06 to fit the figure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

baseline condition in which participants could estimate their position and heading accurately.[6]

In the transportation condition (see Fig. 7A), participants were transported along the paths without any physical travel. Participants extracted travel directions and speeds from the optic flow only. Participants might not have been able to extract either accurate rotation or accurate translation information from the optic flow of the grassland. Because both the heading estimation and the position estimation relied on the estimation of the travel direction and distance, neither measure was accurate. The transportation condition provided a baseline condition under which participants could not estimate their position or their heading accurately.

In the clockwall condition, participants were transported along paths in a way similar to that of participants in the transportation group. However during transportation, participants saw a clockwall surrounding them (see Fig. 7B). The clockwall provided a precise orientation cue. Therefore, participants could estimate their heading accurately. However, the position estimation in the clockwall condition might still have been less accurate than that in the walking condition and might even have been as inaccurate as that in the transportation condition. The reason is that the clockwall was too large to provide translational information, and so it provided only a rotational cue and not a translational one.

In the disorientation condition (see Fig. 7A), participants physically walked paths similar to those in the walk condition, but were disoriented before positioning objects. As path integration was finished before disorientation, participants should have an accurate estimation of the test position. However, their heading estimation should be at chance level, due to disorientation.

If the method of dissociating the position estimation and the heading estimation is empirically valid, the results in Experiment 2 should be aligned with the predictions described above (see Table 3). Furthermore, as the poles were used during the path in all conditions, and if the allothetic information of the travel distance from the poles was critical in heading and position estimations, then heading and position estimations would be as accurate in the transportation condition as in the walking condition.

3.1. Method

3.1.1. Participants

Sixty-four university students (32 men and 32 women) participated in this experiment; participation fulfilled a partial requirement for an introductory psychology course.

3.1.2. Materials and design

The materials are similar to those in Experiment 1. Participants walked five paths in a random order and at the

[6] In this experiment, the term *accurate (inaccurate)* is relative. We used the performance in the walking condition as the accurate performance because it should have been the best performance in all conditions. Similarly, we used the performance in the transportation condition as the inaccurate performance because it should have been the worst performance other than the chance level performance in all conditions.

end of each path, participants needed to replace the five objects using the virtual stick. The turning angles of the paths were 10°, 50°, 90°, 130°, and 170° (all turning left), respectively.

The primary independent variable was the locomotion condition. In the *walking condition*, participants physically walked a two-leg path in a virtual grassland environment. In the *transportation condition*, participants were transported along the two-leg path in the same grassland environment as in the walking condition. In the *clockwall condition*, a clockwall was presented to participants during transportation. As the clockwall was far away in terms of the walking area, it provided precise directional information but not precise positional information. In the *disorientation condition*, participants physically walked the paths as in the walking condition but were disoriented after walking. Sixteen participants (eight men) were randomly assigned to each of the four locomotion conditions.

The primary dependent variables included the absolute pointing error, which was measured as the absolute angular difference between the direction from the test position to the estimated origin (PO′ in Fig. 2) and the direction from the test position to the correct origin (PO in Fig. 2), or β (i.e. PO′–PO); the absolute angular error of the estimated test position, which was the absolute angular difference between the direction from the origin to the estimated test position (OP′ in Fig. 2) and the direction from the origin to the correct test position (OP in Fig. 2), or OP′–OP which is the same as P′O–PO in Eq. (4); the absolute heading error, which was the absolute angular difference between the estimated heading (H′ in Fig. 2) and the correct heading (H in Fig. 2), or H′–H in Eq. (7).

3.1.3. Procedure

3.1.3.1. Walking and rotation speed testing. Before the main experiment, all participants' normal walking and turning speeds were measured; these factors were used as the translational and rotational speeds for participants in the transportation condition and for participants in the clockwall condition (see Table 3). After signing the consent form, participants were blindfolded and led into the experiment room. They then donned the HMD. Participants were led to the starting position. They were then asked to look for a red pole and walked toward it at their normal walking speed. The pole disappeared when participants walked into a circular area, 0.1 m in radius, whose center was the pole. The walking time was measured from the point when participants directly faced the pole to the point when the pole disappeared. In total, participants needed to complete four trials of the walking speed test. The walking distance in each trial was 1.8 m. After the trials were completed, the translational speed was calculated, the translational speed was calculated.

During the rotation speed test, participants were instructed to rotate in place until they directly faced another red pole that was initially behind them. The rotation time was measured from the point when participants started rotation to the point when they finished. They completed four trials of this rotation. The turning angle in each trial was 180°. The rotational speed was calculated accordingly.

3.1.3.2. Path integration task. The origin of each path, which was marked as a red pole (illustrated by O in Fig. 7) was randomly selected from positions with the distance of 1.8 m to the center of the physical room.

In the walking condition and the disorientation condition, participants physically walked toward the red and green poles. In the transportation condition and the clockwall condition, participants were standing without any physical travel but were transported along the path at the translational and rotational speeds measured in the phase of *walking and rotation speed testing.* The simulated eye height was still set to be participants' actual eye height by the motion tracking system (InterSense, Inc., Massachusetts). Participants who were transported were explicitly instructed that they were transported as if they were sitting in a car ("Imagine you are sitting in a car. The car will take you to a new position. After you reach the new position, with a new facing orientation, you need to replace the objects"). The clockwall condition was the same as the transportation condition, except that the clockwall appeared with 12 o'clock facing participants before they were transported along the first leg. The clockwall was present during transportation, providing the orientation cues, and was removed before the testing. The disorientation condition was similar to the walking condition with the following differences: after reaching the green pole, participants sat on a swivel chair and rotated for 30 s. Participants were asked to count backwards, by seven, from a given number. To exclude any acoustic cues for reorientation, white noise was played during the rotation. After the rotation, all participants were turned to face the same testing direction in the real environment (i.e., west in the real environment). Hence, in the disorientation condition, participants' correct test heading (i.e., H) differed from the direction of the second leg (i.e., from T to P).

Standing at the test position and facing the test heading, participants were asked to replace each object, which was probed in a random order. To replace the objects, participants had to use the wand to point the virtual stick at the remembered position. Only one replaced object was visible at a time. No feedback was given. One practice trial with a 100° turning angle was used prior to the five experimental paths.

3.1.4. Data analysis

Using the method explained in the introduction, we calculated one pointing error for the origin (i.e. β or PO′–PO in Fig. 2), four angular errors of position estimation (P′O–PO), and four angular errors of heading estimation (H′–H) for each path and each participant. Because absolute errors were the simplest measure of inaccuracy, the average absolute position error, the average absolute heading error, and the absolute pointing error for the origin for each path and each participant were used in data analyses.

3.2. Results

Absolute position error, absolute heading error, and absolute pointing error as a function of locomotion and turning angle are plotted in Fig. 8A–C, respectively.

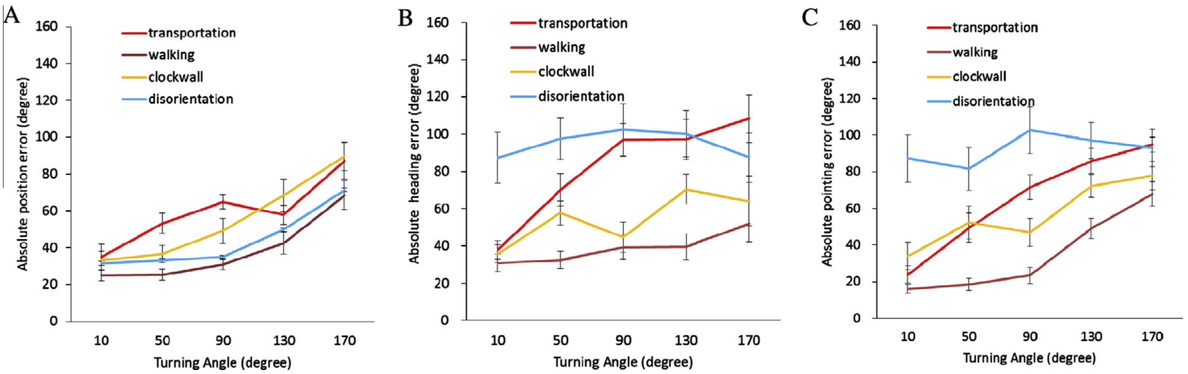

Fig. 8. Absolute position error (A), absolute heading error (B), and absolute error in pointing to the origin (C) as a function of the turning angle in Experiment 1. Error bars represent confidence intervals corresponding to ±1 standard error without removing the individual differences.

3.2.1. Absolute position error

The main effect of the turning angle was significant, $F(4,240) = 38.29$, $MSE = 592.90$, $p < .001$, $\eta_p^2 = .39$. The main effect of locomotion was also significant, $F(3,60) = 7.29$, $MSE = 1058.76$, $p = .001$, $\eta_p^2 = .27$. The interaction between the turning angle and locomotion was not significant, $F(12,240) = 1.03$, $MSE = 592.90$, $p = .42$, $\eta_p^2 = .05$.

Post-hoc Tukey's HSD test showed that estimation of the test position was more accurate in the walking condition than in the transportation and clockwall conditions, $qs(4,60) \geqslant 3.30$, $ps \leqslant .009$, but was not significantly different between the walking condition and the disorientation condition, $q(4,60) = 1.11$, $p = .69$. The position estimation error was not significantly different between the transportation condition and the clockwall condition, $q(4,60) = 0.83$, $p = .84$. It was larger in the transportation condition than in the disorientation condition, $q(4,60) = 3.02$, $p = .02$. The position estimation error was not significantly different between the clockwall condition and the disorientation condition, $q(4,60) = 2.19$, $p = .14$.

In all locomotion conditions, the position estimation error increased linearly with the turning angle, $Fs(1,240) \geqslant 25.22$, $ps < .001$.

3.2.2. Absolute heading error

The main effect of the turning angle was significant, $F(4,240) = 7.96$, $MSE = 1162.74$, $p < .001$, $\eta_p^2 = .12$. The main effect of the locomotion was also significant, $F(3,60) = 16.84$, $MSE = 2939.35$, $p < .001$, $\eta_p^2 = .46$. The interaction between the turning angle and locomotion was significant $F(4,240) = 2.61$, $MSE = 1162.74$, $p = .003$, $\eta_p^2 = .12$.

Post-hoc Tukey's HSD test showed that estimation of the test heading was more accurate in the walking condition than in the disorientation and the transportation conditions, $qs(4,60) \geqslant 5.04$, $ps \leqslant .001$, but was not significantly different between the walking condition and the clockwall condition, $q(4,60) = 1.83$, $p = .27$. The heading estimation was more accurate in the clockwall condition than the transportation condition, $q(4,60) = 3.21$, $p = .01$. The inaccuracy of the heading estimation was not significantly different between the transportation condition and the disorientation condition, $q(4,60) = 1.29$, $p = .57$; the heading estimation was more accurate in the clockwall condition than in the disorientation condition, $q(4,60) = 4.50$, $p < .001$.

The linear trend of the heading error with the turning angle was significant in the transportation condition and in the clockwall condition, $Fs(1,240) \geqslant 6.56$, $ps \leqslant .01$. The linear trend of the heading error with the turning angle was not significant in the walking condition, $F(1,240) = 3.39$, $p = .07$, or in the disorientation condition, $F(1,240) = .02$, $p = .89$.

The heading errors for all five turning angles in the disorientation condition were at chance level; there was no significant difference from 90°, $ts(15) \leqslant .88$, $ps(15) \geqslant .39$.

3.2.3. Absolute pointing error to the origin

The main effect of the turning angle was significant, $F(4,240) = 17.99$, $MSE = 1086.86$, $p < .001$, $\eta_p^2 = .23$. The main effect of the locomotion was also significant, $F(3,60) = 30.47$, $MSE = 2203.70$, $p < .001$, $\eta_p^2 = .60$. The interaction between the turning angle and locomotion was not significant $F(4,240) = 1.43$, $MSE = 1086.86$, $p = .16$, $\eta_p^2 = .07$.

Post-hoc Tukey's HSD test showed that pointing to the origin was more accurate in the walking condition than in the other three conditions, $qs(4,60) \geqslant 3.77$, $ps \leqslant .002$. The accuracy in pointing to the origin was comparable between the clockwall condition and the transportation condition, $q(4,60) = .48$, $p = .96$; pointing to the origin was more accurate in the transportation condition than in the disorientation condition, $q(4,60) = 5.24$, $p < .001$. The pointing performance was more accurate in the clockwall condition than in the disorientation condition, $q(4,60) = 5.72$, $p < .001$.

The linear trend of the pointing error to the origin with the turning angle was significant in all conditions, $Fs(1,240) \geqslant 8.60$, $ps \leqslant .004$.

The absolute errors of pointing to the origin for all five turning angles in the disorientation condition were at chance level (90°), $ts(15) \leqslant 1.74$, $ps \geqslant .10$.

3.3. Discussion

The results showed that the position estimation and the heading estimation were both more accurate in the walking condition than in the transportation conditions.

Furthermore, the accuracy in the position estimation was comparable in the disorientation condition and in the walking condition, whereas the heading estimation was at chance level in the disorientation condition. Accuracy in the heading estimation was comparable in the clockwall condition and in the walking condition, whereas the position estimation was as inaccurate in the clockwall condition as in the transportation condition. These results are consistent with the predictions illustrated in Table 3, indicating that the method that dissociates position estimations and heading estimations is empirically valid.

Furthermore, the position estimation and the heading estimation were much worse in the transportation condition than in the walking condition. This indicates that the poles which were presented to guide the next leg were not efficient allothetic cues for participants to learn the path configuration or to know the origin relative to the test position. Participants in the *RotatedClockwallATtesting* groups of Experiment 1 walked the paths similar to the walking group in Experiment 2. This suggests that participants in the *RotatedClockwallATtesting* groups of Experiment 1 primarily use idiothetic cues during path integration.

4. General discussion

The findings of the current projects indicate that the method for dissociating position estimations and heading estimations works well; the findings of the current projects also favor the theoretical models, stipulating that individuals use an allocentric reference direction to update homing vectors during path integration (Gallistel, 1990; Gallistel & Matzel, 2013; Zhang et al., 2011).

Estimations of individuals' position and heading are critical in human navigation. To understand human navigation, we need to understand how individuals estimate their position and heading. To understand how individuals estimate their position and heading, we need to separately measure the estimations of their position and heading. Activities of place cells and heading cells are measures of animals' position estimation and heading estimation, respectively (Chen, King, Burgess, & O'Keefe, 2013; Valerio & Taube, 2012). Place cells have also been reported using single neuron recording in human patients (Ekstrom et al., 2003). Neuroimaging studies have also shown that different human brain areas are related to position estimations and heading estimations (Vass & Epstein, 2013). However, precise neural measurements of humans' estimations of position and heading are still not available for individuals who physically move in the environment. Many studies have used homing performance (e.g., directional error, position error) to understand human path integration at the behavioral level (Loomis et al., 1993). To our knowledge, no previous studies have separated human position estimation and heading estimation when individuals stay at positions other than the origin except for some special cases (Klatzky et al., 1998).The current study is the first of its kind. We believe it is a powerful tool to advance our understanding of human spatial memory and navigation.

Using this method, we obtained novel findings, which might otherwise have been difficult to obtain. In Experiment 1, the results in the *T_RotatedClockwallATtesting* condition, where a rotated clockwall was presented during the test, showed that the estimated last travel direction and the estimated test heading differed. Because the estimated last travel direction determined the estimated test position, we used the estimated test position to infer the estimated last travel direction. The results showed that the estimated last travel direction was determined by the idiothetic cues during walking. In particular, the estimated last travel direction was 50°, the same as participants' turning angle. In contrast, the estimated test heading was determined by the rotated clockwall that was presented during the test. In particular, the estimated test heading was 150°, the same as the heading indicated by the rotated clockwall. We cannot imagine how these results could have been demonstrated if we could not separately measure individuals' estimations of position and heading.

These results are not only novel; they are theoretically important, as they highlight two different theories regarding how individuals update the homing vector during locomotion. The egocentric homing vector model stipulates that the homing vector is encoded in terms of individuals' body coordinate systems (Benhamou et al., 1990; Fujita et al., 1990; Wang & Spelke, 2002). This conjecture implies that individuals can point to the origin without determining their heading after walking the path. Therefore, this model predicts that participants' estimated test heading should be the same as their estimated last travel direction. In contrast, the allocentric homing vector model stipulates that the home vector is encoded in terms of a fixed reference direction in the environment (Gallistel, 1990; Gallistel & Matzel, 2013; Zhang et al., 2011). This conjecture implies that individuals need to determine their heading relative to the fixed reference direction when they need to point to the origin because pointing is egocentric. The rotated clockwall presented after walking might affect their estimation of the test heading such that the estimated test heading is not the same as the estimated last travel direction and is instead aligned with the rotated clockwall. Clearly, the results showed that the estimated last travel direction and the estimated test heading differed in the *T_RotatedClockwallATtesting* condition, thus supporting the allocentric homing vector model rather than the egocentric homing vector model.

The results in the *R+T_RotatedClockwallATtesting* condition also support the allocentric homing vector model rather than the egocentric homing vector model. Participants rotated 720° such that their idiothetic cues could not predict their last travel direction accurately. Because the estimated last travel direction determined the estimated test position, we used the estimated test position to infer the last travel direction. The results showed that the estimated test position was random across participants without any preferred direction in terms of the origin, confirming that the estimated last travel direction was random across participants. According to the allocentric homing vector model, participants determined their heading when they indicated the origin. As a result, their heading would have been influenced by the rotated clockwall that was presented during testing. According to the egocentric homing vector model, participants did not need to determine their heading relative to the environment when they indicated the origin, given that the direction of the origin was already encoded in terms of their body coordinate systems during locomotion. Thus, their estimated test heading should have been the same as their estimated last travel direction. Because participants' estimated last travel direction was random across participants, their estimated test heading should have been random as well. The results showed that the estimated test heading was not random. Instead, the estimated test heading was consistent with the heading indicated by the rotated clockwall. Therefore, these results also suggest that individuals update their homing vector in terms of a fixed reference direction in the environment rather than in terms of their heading during locomotion.

Interestingly, insects also use a fixed reference direction to update their homing vectors (Menzel et al., 2011). Ants use polarized sunlight to determine their travel direction relative to the sun's azimuth (Müller & Wehner, 1988; Wehner, Michel, & Antonsen, 1996). Bees use magnetic fields to establish a reference direction (Collett & Baron, 1994). There is no evidence that humans can use sunlight or magnetic fields to establish a reference direction. However, humans might use salient environmentally defined axes as reference directions (Shelton & McNamara, 2001). The literature of spatial memory and navigation indicates that individuals can also establish a fixed reference direction using their first-learning direction or travel direction (i.e., the direction of the first leg of a path) (Mou et al., 2013; Richardson, Montello, & Hegarty, 1999; Shelton & McNamara, 2001). We hypothesize that participants in the current study might have used their first travel direction to establish a fixed reference direction. When they made turns, the new travel vector was encoded in terms of the fixed reference direction and added to the previous homing vector in terms of the same fixed reference direction to get the new homing vector.

Another important finding in Experiment 1 was that both allothetic cues (i.e., the rotated clockwall) and idiothetic cues can affect the estimation of the travel direction. The importance of cues depends on the reliability of the cues (Etienne & Jeffery, 2004; Foo et al., 2005). When participants had an accurate idiothetic cue and an inaccurate clockwall in the *T_RotatedClockwallAT2ndleg* condition, they used the idiothetic cue to estimate their last travel direction. When the reliability of the idiothetic cue was eliminated or impaired in the *R+T_RotatedClockwallAT2ndleg* condition, participants used the rotated clockwall instead to estimate their travel direction.

The relative importance of cues also depends on whether the cues were presented during or after locomotion. Although the idiothetic cues were dominant in determining the estimated travel direction during locomotion, the allothetic cue (i.e., the rotated clockwall) appeared to be the more important cue to reset the estimated test headings after locomotion. This interaction further suggests that the estimation of the travel direction during locomotion and the estimation of the test heading after locomotion are two separate mechanisms. This conclusion was consistent with one previous finding (Klatzky et al., 1998), in which participants in the transportation condition accurately estimated their last travel direction but used their actual heading to point to the origin.

This project described a method that separately measures the estimations of participants' position and heading leading to some novel findings. However, we acknowledge one limitation of this method. This method requires the measurement of the angle of PO′X′ (Fig. 2). Therefore individuals need to indicate the locations of O′ and X′ to get the directions of PO′ and the direction of O′X′. In some scenario, we may only be able to get the directions of O′ and X′ but not the locations of O′ or X′. For example, in a large scale environment, individual may only be able to indicate the direction of a target rather than the distance of the target. Thus, the angle of PO′X′ cannot be measured if we only have the directions of O′ and X′. Accordingly, other methods that do not require distances estimations should be developed to address this limitation.

In summary, the current project introduced a method of dissociating position estimations and heading estimations. When the idiothetic cues were reliable during walking, individuals used idiothetic cues instead of the rotated visual orientation cue to determine their last travel direction. In contrast, after walking, individuals used the rotated visual orientation cue to reset their heading whether or not idiothetic cues during walking were reliable. These results indicated that the estimated last travel direction and the estimated test heading differed when the rotated visual orientation cue was presented during the test, supporting the theory that individuals update the homing vector in terms of a fixed reference direction rather than in terms of their body coordinate systems (i.e., their heading).

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Appendix A

As $\angle PO'X' = P'OX$ (see Fig. A1), we get:

$$\angle MOX = \angle M'O'X' \quad (8)$$

Note that the $\angle$ in this and all following equations refers to the clockwise angular distance from the first line of the angle to the second line of the angle. For example $\angle MOX$ is the clockwise angular distance from OM to OX.

$$P'O - PO = \angle NOM = 360^\circ - \angle MOX - \angle XON \quad (9)$$

Replacing $\angle MOX$ with $\angle M'O'X'$ in Eq. (9) according to Eq. (8), we get:

$$P'O - PO = \angle NOM = 360^\circ - \angle M'O'X' - \angle XON \quad (10)$$

We refer to $360^\circ - \angle XON$ (i.e. $\angle NOX$) in Eq. (10) as α and refer to $\angle M'O'X'$ as α' (see Fig. A1). Hence,

$$P'O - PO = \angle NOM = \alpha - \alpha' \quad (11)$$

Because participants replace the object at the origin to O′ while standing at P and facing H when they think they are replacing it to O while standing at P′ and facing H′, we get the following formula:

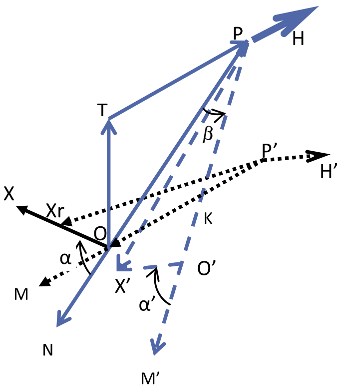

Fig. A1. Dissociating heading estimations and position estimations using the errors in pointing to the origin (O) and to another object (X). A hypothetical participant walks a two-leg path, starting from O (origin), turning at T (turning), and ending at P (test position). The participant's test heading is referred to as H. The represented position of X during learning is Xr. The estimated position of Xr is X′. The estimated position of O is O′. The estimated test position is P′, and the estimated test heading is H′. P′M is the extended line for P′O; PN is the extended line for PO; and PM′ is the extended line for PO′. K is an intersection point of the line of P′O and PM′. $\alpha = \angle NOX$; $\alpha' = \angle M'O'X' = \angle MOX$; $\beta = -\angle O'PO$.

$$PO' - H = P'O - H' \tag{12}$$

Hence,

$$H' - H = P'O - PO' = KO - KO' = \angle O'KO = \angle POP' + \angle O'PO \tag{13}$$

As $\angle POP' = \angle NOM = \alpha - \alpha'$, $\angle O'PO = -\beta$, we get

$$H' - H = \alpha - \alpha' - \beta \tag{14}$$

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