



Selective resetting position and heading estimations while driving in a large-scale immersive virtual environment

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Received: 13 July 2018 / Accepted: 24 October 2018 / Published online: 8 November 2018
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Abstract

Two experiments investigated how self-motion cues and landmarks interact in determining a human's position and heading estimations while driving in a large-scale virtual environment by controlling a gaming wheel and pedals. In an immersive virtual city, participants learned the locations of five buildings in the presence of two proximal towers and four distal scenes. Then participants drove two streets without viewing these buildings, towers, or scenes. When they finished driving, either one tower with displacement to the testing position or the scenes that had been rotated reappeared. Participants pointed in the directions of the five buildings. The least squares fitting method was used to calculate participants' estimated positions and headings. The results showed that when the displaced proximal tower reappeared, participants used this tower to determine their positions, but used self-motion cues to determine their headings. When the rotated distal scenes reappeared, participants used these scenes to determine their headings. If they were instructed to continuously keep track of the origin of the path while driving, their position estimates followed self-motion cues, whereas if they were not given instructions, their position estimates were undetermined. These findings suggest that when people drive in a large-scale environment, relying on self-motion cues, path integration calculates headings continuously but calculates positions only when they are required; relying on the displaced proximal landmark or the rotated distal scenes, piloting selectively resets the position or heading representations produced by path integration.

Keywords Self-motion cues · Landmarks · Driving · Heading estimations · Position estimations

Introduction

Knowing our positions (where we are located) and headings (which direction we are facing) in an environment is important for successful navigation, such as planning a route from our current position to home. We use two navigation methods to estimate (update) our positions and headings: path integration and piloting (Etienne et al. 1999; Gallistel 1990; Gallistel and Matzel 2013). Path integration relies on self-motion cues to obtain our current moving directions and distances, adds these new directions and distances to the previously estimated positions and headings, and then updates estimates of our positions and headings (Etienne and

Jeffery 2004; Loomis et al. 1999; Mittelstaedt and Mittelstaedt 1980). Self-motion cues comprise optic flow and idiothetic cues. The latter includes vestibular cues, proprioceptive cues, and motor efference copies. Piloting, also called landmark-based navigation, uses previously encoded visual landmarks in the environment to determine our positions and headings (e.g., Cheng and Spetch 1998; Etienne et al. 1996, 2004; Foo et al. 2005; Wehner et al. 1996). Several studies have examined the roles of path integration and piloting in position and heading estimations when participants walk in a small space (e.g., Mou and Zhang 2014; Zhang and Mou 2017). The purpose of the current study, however, was to examine the roles of path integration and piloting in position and heading estimations when people drive in a large-scale immersive virtual environment by controlling a gaming wheel and pedals.

In everyday life, people usually see visual landmarks while walking around. Therefore, piloting using landmarks and path integration using self-motion cues usually work together in updating people's positions and headings. One

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popular theory about the roles of these two methods in people's estimations of positions and headings is that path integration dynamically updates estimates of people's positions and headings, whereas piloting intermittently corrects the errors accumulated in path integration (Etienne and Jeffery 2004; Gallistel 1990; but see, Tcheang et al. 2011). Many studies have demonstrated that people dynamically update estimates of their positions and headings using self-motion cues (Loomis et al. 1993, see 1999 for a review; Rieser 1989). Studies also suggest that path integration is not only dynamic but also automatic (Farrell and Robertson 1998; May and Klatzky 2000). However, path integration involves errors (Fujita et al. 1993; Maurer and Séguinot 1995). Errors in path integration could be accumulated quickly with the increase in the number of turns if there are no external cues (Benhamou et al. 1990; Kelly et al. 2008). But when there are external landmarks, the visual landmarks can remove errors in the path integration of humans (e.g., Kelly et al. 2008) and non-human animals (see Etienne et al. 1996, 2004; Etienne and Jeffery 2004 for reviews). This error-correcting process is called resetting (Etienne et al. 2004).

A homing task is widely used to study path integration. In particular, participants walk an outbound path (usually with two legs and one turn between the legs) and then judge the origin of the path (Loomis et al. 1999). Participants point to the origin of the path or walk back to the origin. The vector (direction and distance) from participants' testing positions to the estimated position of the origin is referred to as the homing vector. To study the interaction between path integration and piloting in human homing behaviors, a cue conflict paradigm is usually used (e.g., Chen et al. 2017; Nardini et al. 2008; Zhao and Warren 2015). In particular, before participants walk toward or point to the origin in the homing task, the visual landmarks in the environment are displaced or rotated, therefore indicating a home location different from that indicated by path integration. If participants estimate the home location based primarily on the displaced or rotated landmarks, the conclusion is that landmarks are dominant over self-motion cues and landmarks reset path integration (e.g., Zhao and Warren 2015).

Mou and Zhang (2014) argued that examining interaction between piloting and path integration in homing estimation might not exactly reflect how piloting and path integration interact in estimating position and heading. The argument is based on the observation that we cannot separate position and heading estimates at the end of the outbound path using a home estimate because people's homing estimates are jointly determined by their estimates of positions and headings at the end of the outbound path. Angular errors in both heading and position estimates contribute to angular errors in homing estimates (homing error = position error – heading error; see the "Appendix"). With the measured homing errors, we cannot

separate contributions from position errors and heading errors. Thus, the findings about cue interaction between piloting and path integration in homing estimation cannot precisely illustrate how piloting and path integration affect people's estimations of their positions and headings at the end of the outbound path.

Mathematically, the difficulty in calculating position errors and heading errors using the observed homing error is that we cannot use one measured error (i.e., homing error) to infer two unknown errors (i.e., position errors and heading errors). Extending the homing paradigm, Mou and Zhang developed a paradigm in which participants learned the locations of at least two objects (one at the origin and the other at a location in addition to the origin) and then replaced the two objects after walking an outbound path. With two measured errors in replacing two separate objects, the position error and heading error at the end of the outbound path can be calculated (see the "Appendix" and Mou and Zhang (2014) for details of the calculation).

More relevant to the current study, participants in Mou and Zhang (2014) learned the locations of objects in the presence of distal landmarks and then walked the outbound path towards the testing position after the distal landmarks and objects disappeared. Before participants replaced the objects, the distal landmarks reappeared with a rotation of 100°. The estimated positions and headings of participants were calculated from the replaced locations of the objects. The results showed that the estimated headings of participants were determined by the rotated distal landmarks, whereas their estimated positions were still determined by path integration. Furthermore, in Zhang and Mou (2017), participants learned objects in the presence of a proximal landmark and then walked the outbound path towards the testing position after the landmark and objects disappeared. Before participants replaced the objects, the proximal landmark reappeared and had been displaced to the testing position. The results showed that the estimated position of participants was determined by the displaced landmark, whereas the estimated heading of participants was still determined by path integration.

These two studies suggest: (a) that people separately maintain their position and heading representations, (b) that both representations are dynamically updated by path integration while walking, and (c) that the heading or position representations from path integration can be reset selectively by rotated distal cues or by a proximal landmark displaced to the testing position. Rotated distal cues do not reset the position estimates from path integration, because distal cues alone cannot specify a location. The proximal landmark displaced to the testing position does not reset the heading estimates from path integration, because it alone cannot specify a direction. We refer to this elaborated resetting model as the selective resetting hypothesis to differentiate it from the

original resetting theory (Etienne and Jeffery 2004; Gallistel 1990).

In the current study, we tested the selective resetting hypothesis when participants drove in a large-scale immersive virtual environment by controlling a gaming wheel and pedals while donning a head-mounted display (HMD). There are two important theoretical motivations. The first motivation is to investigate whether the selective resetting hypothesis can be generalized to a different environment scale and a different locomotion mode. The second motivation is to investigate whether the claims of dynamic updating of positions and headings from path integration depend on locomotion mode.

With regard to the first theoretical motivation, in previous studies (Mou and Zhang 2014; Zhang and Mou 2017), participants walked within a small-scale immersive virtual environment (approximately 4×4 m). The environment scale (small versus large) and the locomotion mode (walking versus driving) may impact the interaction between piloting and path integration, as human spatial cognition in general depends on the environment scale (Montello 1993) and the locomotion mode (Klatzky et al. 1998).

On one hand, the interaction between piloting and path integration in a large-scale environment may differ from that in a small space. In a small space, people usually see all items while standing in a single position. Therefore, the role of piloting might be critical, whereas the role of path integration is trivial to updating of positions and headings in a small space. In contrast, in a large-scale environment, people cannot view all items while standing in a single position and need to locomote to view them. As a result, estimating positions and headings is more challenging in piloting and thus requires more contributions from path integration in the large-scale environment than in a small space (e.g., Ishikawa and Montello 2006).

On the other hand, the interaction between piloting and path integration while driving may also differ from that while walking (Waller et al. 2003, 2004). Waller et al. (2003) showed that spatial knowledge of participants who were sitting in a car while donning an HMD and acquired spatial knowledge through a car trip in a large-scale environment was compared with participants who were sitting in a laboratory and learned the same environment by watching the video taken from the car trip. In contrast, Waller et al. (2004) reported that the spatial knowledge of a large-scale environment was better when participants walked in the environment while donning an HMD than when participants were sitting in the laboratory and watched the video that had been taken while walking. These studies indicated that self-motion cues available while walking but not while driving might be critical to spatial learning. As optic flow and inertial (vestibular) cues are available while both driving and walking but proprioceptive cues are only available while

walking, proprioceptive cues might be critical to spatial learning. Furthermore, Chrastil and Warren (2013) reported that proprioceptive cues are critical to spatial learning via path integration. Hence, path integration may be much less efficient while driving than while walking due to the lack of proprioceptive cues while driving. In addition, compared with driving in the physical world, participants driving in an immersive environment even do not have inertial cues, which might make the spatial learning from path integration even harder in driving in an immersive environment (e.g., Klatzky et al. 1998).

Therefore, it is not clear whether the selective resetting heading/position estimates from distal/proximal landmarks, observed when participants walked in a small space, can be generalized to a situation in which participants drive in a large-scale immersive virtual environment by controlling a gaming wheel and pedals. As the selective resetting of heading or position estimates is the core claim of it, the selective resetting hypothesis will be much strengthened if selective resetting occurs regardless of the scale of the environment (small or large) and the locomotion mode (driving by controlling a gaming wheel and pedals, or walking).

With regard to the second theoretical motivation of our research design (investigating whether the claims of dynamic updating of positions and headings from path integration depend on locomotion mode), we speculate that the claim of dynamic updating of positions and headings might not be true when people drive in an immersive environment by controlling a game wheel and pedals. The resetting hypotheses, both the original resetting hypothesis and the selective resetting hypothesis, claim that path integration continuously calculates one's positions and headings. However, spatial updating by path integration might be less efficient while driving in immersive virtual environment than while walking (Waller et al. 2003, 2004) due to the lack of idiothetic information (Chrastil and Warren 2013; Klatzky et al. 1998). As a consequence, path integration might not be able to continuously update positions and headings of individuals as proposed in the resetting hypotheses.

Furthermore, Loomis and his colleagues (1999) proposed that spatial updating of the homing estimates might not always be continuous. In addition to continuous spatial updating, people may represent the travel distances and turning angles during locomotion instead of calculating the homing vector continuously. They calculate the homing vector only when they reach the end of the outbound path (referred to as configural updating). Configural updating more likely occurs when the path complexity increases, suggested by the findings that latency in homing increased with the number of turns in the outbound path. In addition, Wiener et al. (2011; see also He and McNamara 2017) showed that homing estimates were continuously updated when participants were asked to keep track of the origin of the outbound path

during locomotion, whereas homing estimates were only updated at the end of the outbound path when participants were asked to pay attention to the shape of the outbound path while walking.

Inspired by these theoretical ideas and empirical findings, we hypothesize that path integration updates people's position estimates continuously while walking but not continuously (i.e., only when required) while driving; by contrast, path integration updates people's heading estimates continuously regardless of the locomotion methods (walking or driving). We assume that whether people continuously update spatial representations (estimates of their positions and headings) or not depends on the difficulty of updating spatial representations. People more likely continuously update spatial representations when difficulty of doing so is lower (e.g., Loomis et al. 1999). Moreover, the difficulty of updating spatial representations is jointly determined by both computational complexity of spatial updating and self-motion cues available during locomotion. We conjecture that computational complexity of updating position estimates is much higher than that of updating heading estimates. However, this difference in terms of computational complexity could be attenuated by rich idiothetic cues that are available while walking but not available while driving.

During locomotion (whether walking or driving in immersive virtual environments), computational complexity of updating individuals' position estimates is much higher than that of updating individuals' heading estimates. In path integration, position estimations during locomotion rely on heading estimations. Path integration calculates the new heading estimate only by updating the new travelling direction but calculates the new position estimate by adding the new travelling vector (travelling distance in the travelling direction) to the previous position estimate. By contrast, in path integration, heading estimations do not rely on position estimations. Because of this asymmetrical dependency between position and heading estimations, estimating one's position is much more complex than estimating one's heading.

However, the difficulty of estimating positions compared with estimating heading might not be significant or noticeable when participants walk, but becomes significant and noticeable when participants drive (controlling a gaming wheel and pedals). Individuals have rich idiothetic cues while walking. By contrast, while driving in immersive virtual environment, idiothetic cues are rare and optic flows might be the primary self-motion cues. Rich idiothetic cues might lead to effortless or automatic spatial updating whereas optic flows may not (e.g., Chrastil and Warren 2013; Klatzky et al. 1998; Rieser 1989; Ruddle and Lessels 2009). Consequently, rich idiothetic cues available while walking might attenuate the differences in computational complexity between estimating positions and headings, and therefore

support the continuous updating of both positions and headings while walking. By contrast, because there are rare idiothetic cues while driving (by controlling a game wheel and pedals), updating position and heading estimates might not be automatic and requires cognitive effort. Consequently, the computational complexity significantly influences the difficulty of spatial updating. Thus, spatial updating of heading estimates might be continuous due to the low computational complexity of heading estimations, whereas spatial updating of position estimates might not be continuous and occur only when required while driving due to high computational complexity of position estimations.

Given that the mechanism of position updating (i.e., continuous versus only when required) in path integration might depend on the locomotion mode, we modify the selective resetting hypothesis. In the modified version, when people drive by controlling a game wheel and pedals, path integration produces heading estimations continuously but produces position estimations only when required, whereas when people walk, path integration produces both heading and position estimations continuously. By contrast, according to the original selective resetting hypothesis, path integration produces both heading and position estimations continuously regardless of walking or driving. Despite this modification, the heading or position representations from path integration can still be reset selectively by rotated distal cues or by a displaced proximal landmark when people drive. We refer to this modified hypothesis as the locomotion-dependent selective resetting hypothesis. Table 1 summarizes the similarities and differences between these two hypotheses (with differences highlighted in italics). Two experiments were conducted to test the selective resetting hypothesis and the locomotion-dependent selective resetting hypothesis.

Experiment 1

In an immersive virtual city, participants donning a HMD learned the locations of five buildings in the presence of four distal scenes and two proximal towers (illustrated in Figs. 1a, 2a). Without viewing these buildings, scenes, and towers, they then drove on a street, turned at one intersection, and drove on a second street by controlling a gaming wheel and pedals. Some irrelevant buildings were presented on the street to provide rich optic flow and to block the complete view of the shape of the driving path (Fig. 1b). After driving, participants who were standing at the end of the second street (i.e., *P*) and facing in the travelling direction of the second street (i.e., *h*) pointed to the five buildings in different cue conditions. In the no-piloting cue condition (Figs. 1c, 2b), no landmarks reappeared. In the displaced proximal landmark condition (Figs. 1d, 2c), one of the towers was displaced and reappeared at the testing position. In

Table 1 Similarities and differences between the selective resetting hypothesis and the locomotion-dependent selective resetting hypothesis on when path integration updates position and heading estimates

	Selective resetting hypothesis	Locomotion-dependent selective resetting hypothesis
Updating heading representations using self-motion cues	Continuously	Continuously
<i>Updating position representations using self-motion cues</i>	<i>Continuously</i>	<i>Only when required</i>
Resetting heading representations by rotated distal landmarks	Yes	Yes
Resetting position representations by displaced proximal landmarks	Yes	Yes

Differences are highlighted in italics

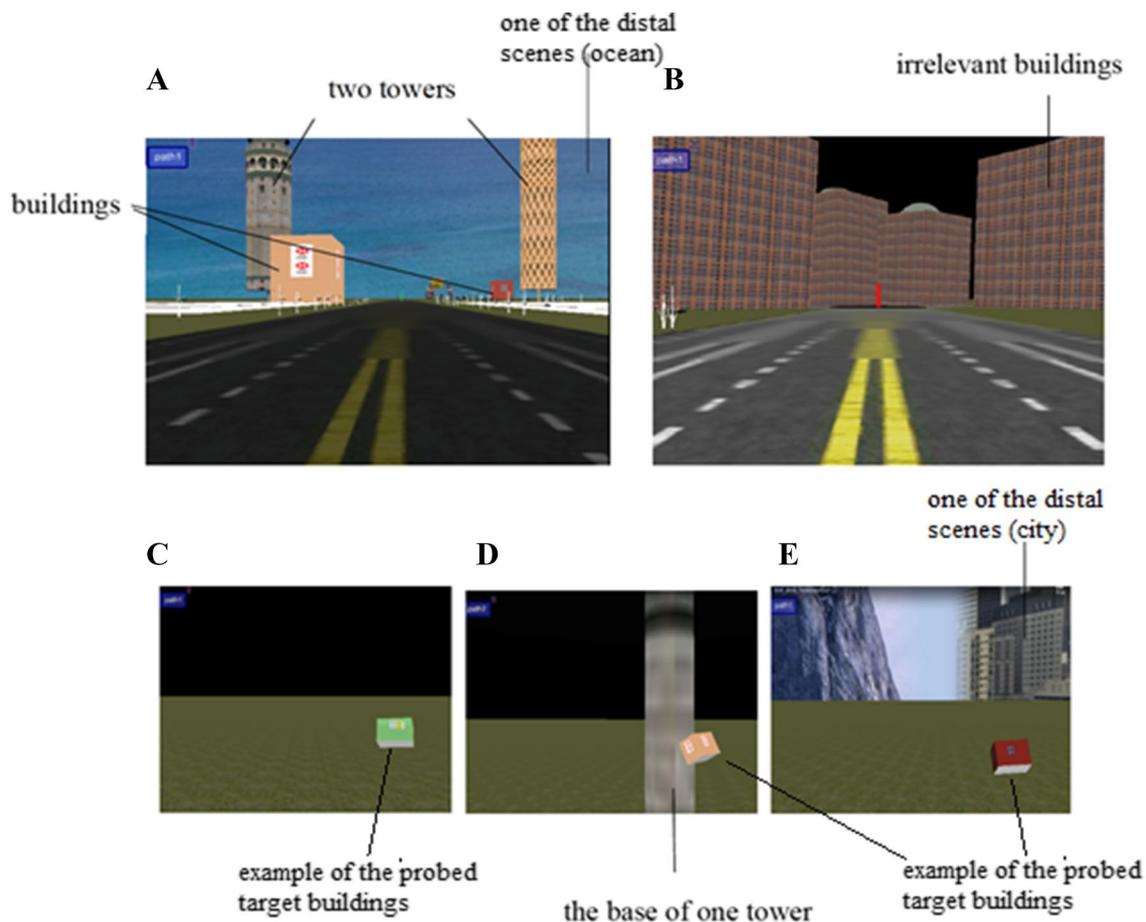


Fig. 1 Snapshots of the first-person view in each experimental phase in Experiment 1 across conditions: the study phase (a), the driving phase (b), the testing phase in the no-piloting cue condition (c), the

testing phase in the displaced proximal landmark condition (d), and the testing phase in the rotated distal scene condition (e)

the rotated distal scene condition (Figs. 1e, 2d), the distal scenes were rotated and reappeared.

We calculated participants’ estimated positions (P') and headings (h') using the least squares method to fit their

responses of the directions of the buildings.¹ The direction

¹ Note that we did not use the method developed in Mou and Zhang (2014), because this method requires people to indicate targets’ locations. In a large-scale environment, however, it is more realistic to point to the targets’ directions.

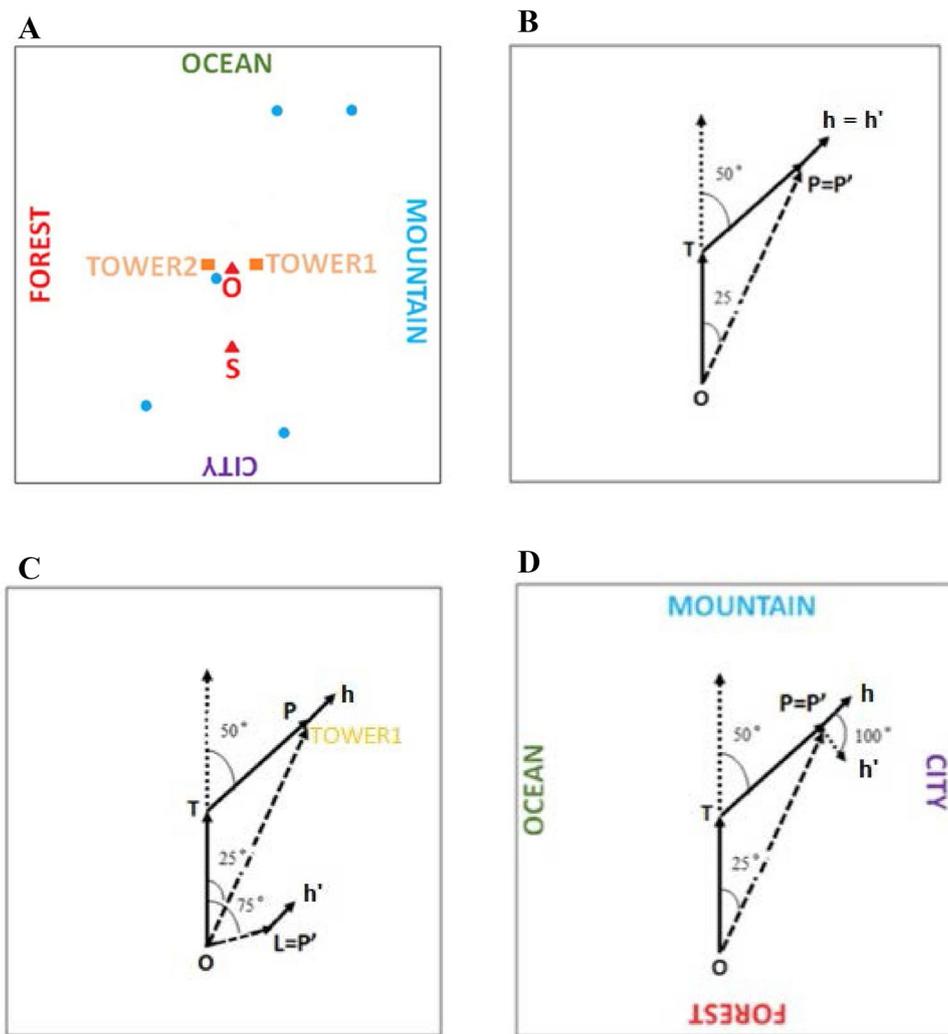


Fig. 2 Schematic diagram of the experimental setup. **a** The study phase across all conditions. The triangles represent the two study viewpoints (S and O). Length of $SO=200$ m. The squares represent the two proximal landmarks (towers 1 and 2). Ocean, forest, city, and mountain represent the distal scenes. All four scenes instead of words were presented. Five dots represent target buildings. **b** No-piloting cue condition. O is the origin of the path. T is the turning point. P is the testing position. h is the testing heading (equivalent to the direction of TP). P' is the estimated position and h' is the estimated heading. According to the selective resetting hypothesis, P' and h' are predicted by self-motion cues and are the same as P and h . **c** Displaced

proximal landmark condition. Tower1 was displaced from L to P during the test. According to the selective resetting hypothesis, P' is reset by the displaced landmark and is the same as L , and h' is predicted by the self-motion cues and is the same as h . **d** Rotated distal scene condition. Distal scenes were rotated 100° during the test. According to the selective resetting hypothesis, h' is predicted by the rotated distal scenes and is 100° from h , and P' is predicted by the self-motion cues and is the same as P . Lengths: $OT=TP=TL=100$ m. Bearings with respect to the direction from O to T : $b_{TP}=50^\circ$, $b_{OL}=75^\circ$, $b_{OP}=25^\circ$

of the estimated heading (h') and the bearing from the origin (O) to the estimated position (P') (in short, $b_{OP'}$) were then used to diagnose whether position and heading estimations followed self-motion cues or piloting cues. Note that we used headings and bearings (both specified as an angle from an allocentric direction in the environment; e.g., the travelling direction on the first street, the direction from O to T in Fig. 2) but not distance as measures to test hypotheses. The use of directions rather than distances is because perceived distance in immersive virtual environments might

be underestimated (Thompson et al. 2004). However, there is no report yet about distortion in direction perception. We summarize the cues available to estimation of the headings and positions in the three conditions in Table 2 (see $b_{OP'}$ and h').

The first purpose of this experiment was to investigate whether resetting also occurred when participants drove in a large-scale immersive virtual environment by controlling a gaming wheel and pedals. The displaced proximal landmark condition was used to investigate whether the displaced

Table 2 Cues that were available to determine the bearing from the origin (*O*) to the testing position (*P*) (in short, *b*_{OP'}) and the estimated testing heading (*h'*), cues that would be used according to the selective resetting hypothesis and the locomotion-dependent selective

resetting hypothesis (predicted), and the cues that were indeed used to determine *b*_{OP'} and *h'* (observed) in different experimental conditions

Conditions	Available cues		Predicted cues		Observed cues	
	<i>b</i> _{OP'}	<i>h'</i>	<i>b</i> _{OP'}	<i>h'</i>	<i>b</i> _{OP'}	<i>h'</i>
No-piloting cue	Self-motion cues	Self-motion cues	Self-motion cues	Self-motion cues	Self-motion cues	Self-motion cues
Displaced proximal landmark	Self-motion and landmarks	Self-motion cues	Landmark	Self-motion cues	Landmark	Self-motion cues
Rotated distal scene	Self-motion cues	Self-motion and landmarks	<i>Self-motion or undetermined</i>	Landmarks	Undetermined	Landmarks
Rotated distal scene and instruction	Self-motion cues	Self-motion and landmarks	Self-motion cues	Landmarks	Self-motion cues	Landmarks

The first three conditions were used in Experiment 1 and the last condition was used in Experiment 2. Note that the selective resetting hypothesis and the locomotion-dependent selective resetting hypothesis have a similar prediction on which cue would determine *b*_{OP'} and *h'* except for *b*_{OP'} in the rotation distal scene condition (highlighted in italics). The former predicts that the *b*_{OP'} would be determined by the self-motion cue whereas the latter predicts that the estimated position would not be determined by self-motion cues and might be undetermined

proximal landmark reset participants' position estimates. In this condition, as the proximal landmark (tower) was displaced to the testing position (from the location of *L* to *P* in Fig. 2c), the positions determined by self-motion cues available in driving were in conflict with those available by the proximal landmark (*P* versus *P'* in Fig. 2c). If participants' positions followed the displaced proximal landmark, then we would conclude that the proximal landmark had reset the participants' position estimates from path integration. The rotated distal scene condition was used to investigate whether the rotated distal scenes reset participants' heading estimations. In this condition, as the distal scenes were rotated 100° in the testing phase (Fig. 2d), the headings determined by self-motion cues available while driving and by the rotated distal scenes reappearing at testing were in conflict (*h* versus *h'* in Fig. 2d). If participants' heading followed the rotated distal scenes, then we would conclude that distal landmarks had reset participants' heading estimations from path integration.

As the locomotion-dependent selective resetting hypothesis follows the original selective resetting hypothesis regarding the selective resetting mechanism (see Table 1), both hypotheses predicted that the displaced proximal landmarks (towers) would determine the position estimation in the condition of displaced proximal landmark (predicted cues for *b*_{OP'} in Table 2) and that the rotated distal landmarks (scenes) would determine the heading estimation in the condition of rotated distal scene (predicted cues for *h'* in Table 2).

The second purpose of this experiment was to investigate whether updating estimates of positions and headings occur continuously or only when required. We examined the estimated heading, *h'*, in the displaced proximal landmark condition and the estimated position, *b*_{OP'}, in the rotated distal scene condition. Because both the selective resetting

hypothesis and the locomotion-dependent selective resetting hypothesis predict that path integration updates heading continuously, the estimated headings (*h'*) in the condition of displaced proximal landmark should follow self-motion cues (see predicted cues for *h'* in Table 2).

However, the selective resetting hypothesis and the locomotion-dependent selective resetting hypothesis have different predictions for position estimation (i.e., *b*_{OP'}) in the rotated distal scene condition. The selective resetting hypothesis claims that path integration continuously produces people's position estimates in driving as in walking. According to this hypothesis, participants' position estimates have been produced continuously in driving by path integration before the rotated distal scenes reappear. Consequently, participants' position estimations would follow self-motion cues available in driving. In contrast, the locomotion-dependent selective resetting hypothesis claims that path integration produces people's position estimates only when required. According to this hypothesis, when participants stop driving, path integration has not yet updated the position representation using self-motion cues and has only encoded the moving distances and turning angle of the path. Furthermore, the rotated distal scenes, reappearing when participants stop driving, disrupt the position calculation in path integration. The rotated distal scenes indicate a turning angle that conflicts with that indicated by self-motion cues. Path integration might not be able to decide which turning angle should be used as the previous travelling direction for the position calculation. As there was no position representation updated yet in path integration when participants stopped driving and no further position estimates could be calculated accurately due to the disruptions from the rotated distal scenes, the position estimates would not follow self-motion cues and might be random (or undetermined). This

key difference in predicted position estimations (predicted cues for b_{OP}) in the rotated distal scene condition between these two hypotheses is highlighted in italics in Table 2.

We also used the no-piloting cue condition as a baseline to measure how accurately participants could primarily use self-motion cues to update their positions and headings in our experimental setup. Participants in our experimental setup primarily used optic flow as self-motion cues. Waller et al. (2003) showed that participants were able to use optic flow to estimate the locations of objects (see also Kearns et al. 2002; Riecke et al. 2007). Other studies, however, showed that optic flow was insufficient for spatial updating (Klatzky et al. 1998; Ruddle and Lessels 2009). Hence, although we know the theoretical values of the position and heading estimations that follow self-motion cues, it is also important to empirically measure these values and show if the empirical values are consistent with the theoretical values. In addition, the consistency between the empirical measurements and the theoretical values can also ensure that our method (the least square fitting) to calculate participants' position and heading estimations is valid.

Method

Participants

Thirty-six university students (18 men and 18 women) participated in the experiment to fulfill a partial requirement for an introductory psychology course. Before the experiment, all participants signed the consent form approved by the University of Alberta Research Ethics Board. We used 36 participants in total so 12 for each cue condition following the same number of participants that had been used in the previous studies (Mou and Zhang 2014; Zhang and Mou 2017).

Materials and design

The virtual city was displayed in stereo with an nVisor SX60 head-mounted display (HMD) (NVIS, Inc., Virginia), with 1280×1024 24-bit color pixels per eye, a 60° diagonal field of view, and a 60 Hz refresh rate. Participants used a gaming wheel and pedals from Logitech Driving Force GT (Logitech International S.A., California) for driving. Their head motions were tracked with an InterSense IS-900 motion tracking system (InterSense, Inc., Massachusetts). Therefore, participants could turn their heads to change their viewing directions while driving the virtual car in the environment, although the travelling direction of the virtual car was only determined by the gaming wheel (for turning) and pedals (for moving forwards or backwards). Participants also used an InterSense IS-900 Wand to control a virtual stick for pointing to the directions of the buildings. The virtual

stick is a colorful stick, extending from the location of the InterSense IS-900 Wand in the virtual environment. Participants could move the wand to change the orientation of the virtual stick and indicate their response of a direction or a location in the virtual environment, analogous to using a mouse to move a cursor to indicate a position on a computer screen.

In the virtual city (Fig. 1), five buildings (7–11, DQ, Subway, HSBC, and NQ) were used as the targets that participants pointed to in the testing phase. Four different scenes (ocean, forest, mountain, and city) were used as distal landmarks, and two different towers (a gray tower and a golden tower) were used as proximal landmarks. We raised the towers up on narrow stalks so that participants in the displaced proximal landmark condition could see themselves standing at the base of the tower in the testing phase. To encourage participants to perceive the locations of the buildings and towers more accurately, we had participants perceive them at two viewing locations: the starting position (S) and the origin of the driving path (O). The distance between these two positions was 200 m.

The four different scenes were set at infinity as distal orientation cues. The two towers were located 51.76 m from O in the direction of 75° clockwise (i.e., the golden one on the right in Fig. 1a) and counter-clockwise (i.e., the gray one on the left in Fig. 1a) with respect to the first street (i.e., the direction from O to T in Fig. 2). The five buildings were located 44.72 m, 364.01 m, 443.27 m, 379.47 m, and 360.56 m away from the origin O . The driving path started from O and consisted of two streets (100 m each) and one turn with 50° either left or right. The first street extended the road from S to O . Only the first street was presented to participants in the study phase. Each participant completed two trials in the experiment (driving two paths with either a left or right turn). The order of the trials was randomized.

The primary independent variable was the cues available to participants after driving the path. In the no-piloting cue condition, neither the distal scenes nor the towers were presented (Fig. 2b). In the displaced proximal landmark condition, only the tower that was in the same direction of the turning path (e.g., the golden one on the right in Fig. 1a for the driving path with the right turn) with respect to the first street was presented (Fig. 2c). The tower was displaced to the testing position (i.e., P). Thus, participants saw that they were standing at the base of the tower after driving. If participants used the displaced tower to estimate their position, they would feel that they stood at the original location of the tower (i.e., L in Fig. 2c). In the rotated distal scene condition, the distal scenes reappeared with a rotation of 100° (Fig. 2d). The direction of the rotation was opposite to the turning direction on the path. Thus, if participants used the rotated distal scenes to estimate the turning angle, they would feel that they had turned 150° . Twelve participants (six men and

six women) were randomly assigned to each of the three cue conditions. We used the same number of participants in each cue condition as in the previous studies (Mou and Zhang 2014; Zhang and Mou 2017) (12 participants and each participant had two paths). The dependent variables were the bearings between the origin and the estimated testing positions (i.e., $b_{OP'}$) and headings (h'), which were calculated from participants' pointing directions of the five buildings.

Procedure

Before the experiment, participants were given three minutes to read and memorize a map that contained the five target buildings and two study locations (S and O). Then, while wearing a blindfold to remove any possible influence from viewing the physical room, participants entered the testing room under the guidance of the experimenter. They then removed the blindfold and donned the HMD.

In the immersive virtual reality environment, participants were teleported to the first study location (S). They studied the distal scenes, two towers, and five buildings for 3 min (Figs. 1a, 2a). Then the buildings disappeared. Participants used the wand to point the virtual stick in the directions of buildings for two blocks. Within each block, all five buildings were visually probed (by presenting their small models at the bottom right of the HMD) in a random order. Feedback on the correct location was provided after each pointing. After studying at S , participants drove from S to O and studied the five target buildings for another 30 s followed by the two rounds of pointing and feedback. After studying at O , participants drove a path (O - T - P ; see Fig. 2b–d) without seeing the proximal landmarks (towers), distal scenes, or target buildings. However, some irrelevant buildings were presented on the street to provide rich optic flow and to block the complete view of the shape of the driving path. At the end of the second street (the testing position P), participants pointed to the five target buildings that were visually probed in a random order in one of the three conditions. After that, participants were teleported to S and started the second experimental trial, which was the same as the first one except for the turning direction (left or right) on the path. Before these two experimental trials, participants had one practice trial to familiarize themselves with the procedure. In the practice trial, they learned the locations of two target buildings that were different from those in the experimental trials. In addition, the turning angle of the path was 90° .

Data analysis

We used the least squares fitting method to calculate the estimates of the testing position and heading for each participant on each experimental path. The least squares fitting method is widely used (e.g., in a regression analysis) and

has also been used in estimating people's headings (e.g., Yerramsetti et al. 2013). For each participant and each path, we searched for a position (P') and a heading (h') that led to the least sum of squares of the errors in pointing buildings. The error in pointing to each building is measured with the angular difference between the original direction of this building, relative to this hypothetical position and heading, and the participant's responded direction to this building, relative to the participant's testing position and heading after driving.² For example, given a hypothetical position and heading, the direction from the hypothetical position to building A relative to the hypothetical heading is 90° ; a participant points in the direction of 80° when he or she points to building A; as a result, the error will be 10° . As in our previous studies, we used the bearing from the origin to the estimated position, $b_{OP'}$, as the position measurement (Mou and Zhang 2014; Zhang and Mou 2017). We did not use distance information of P' relative to P or O because the distance perception in virtual environments might be distorted (Thompson et al. 2004). As we were not interested in the turning direction, we flipped the signs of $b_{OP'}$ and h' for the left-turning path and combined them with those of the right-turning one. Therefore, we obtained 24 estimates for $b_{OP'}$ and h' respectively for each cue condition as each of the 12 participants finished two paths.

In the interest of exposition, in the experiment below we used the driving direction on the first street (i.e., the direction from O to T in Fig. 2) as the reference direction (i.e., direction 0°) to specify the testing headings (h and h') and the bearing of the testing positions relative to the origin (b_{OP} and $b_{OP'}$). In all conditions, if participants used self-motion cues to determine their positions and headings, $b_{OP'}$ should be 25° , half of the turning angle, given the equal length of the two legs; h' should be 50° , the turning angle (see Fig. 2b). In the displaced proximal landmark condition, if participants used the displaced tower to determine their positions, $b_{OP'}$ should be 75° , which is the same as the direction from O to the original location of the tower (i.e., L in Fig. 2c). As the displaced tower reappeared at the testing position, it could not provide any orientation information. Consequently, the heading predicted by the displaced tower was undetermined. In the rotated distal scene condition, if participants used the rotated distal scenes to determine their headings, h' should be 150° , as the scenes were rotated 100° in the direction opposite to the turning angle (50°) of the path (see Fig. 2d). As the distal scenes (presented in infinite distances) alone could not specify locations, the position predicted by the distal scenes was undetermined. We

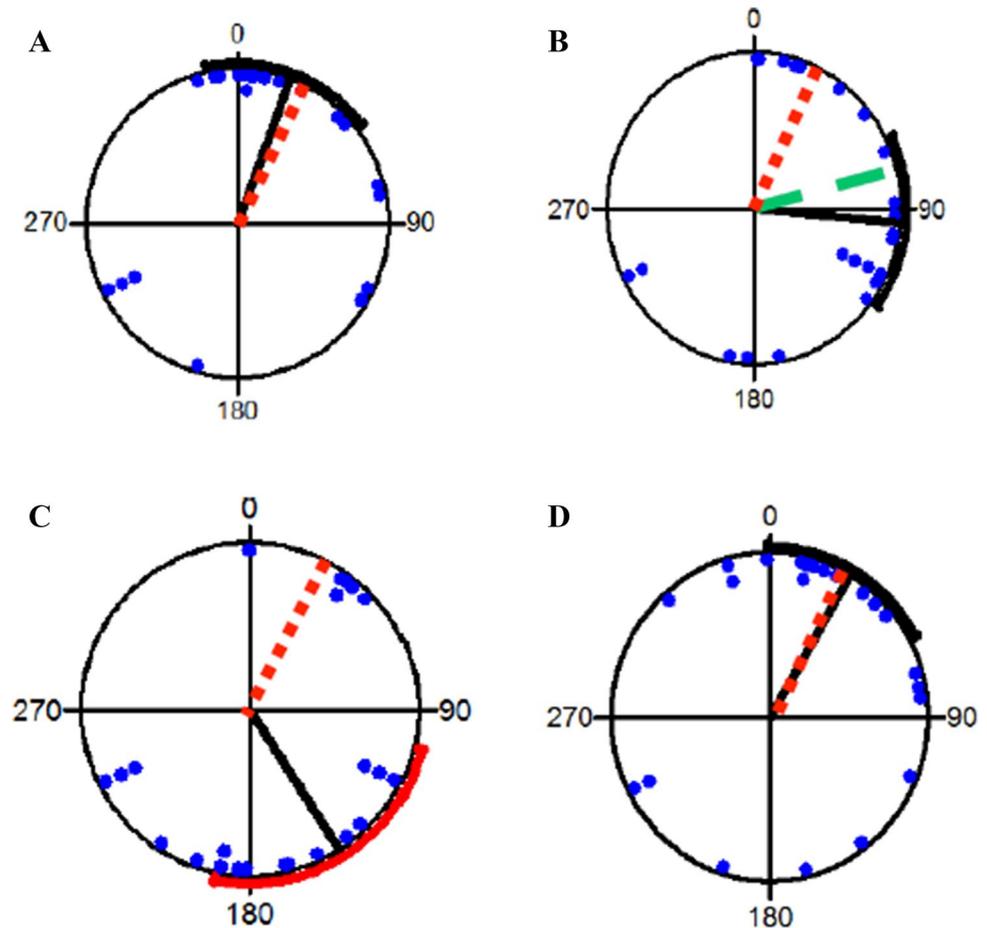
² We used the `fminsearch` function in Matlab as the searching algorithm. Please find the example of the Matlab codes online (<https://doi.org/10.7939/R3057D77Q>).

Table 3 Predicted bearings of the estimated testing position ($b_{OP'}$) and the estimated testing heading (h') based on self-motion cues or landmarks, and the observed $b_{OP'}$ and h' in different experimental conditions

Conditions	Prediction from self-motion cues		Prediction from landmarks		Observed circular mean (length of mean vector, r)	
	$b_{OP'}$	h'	$b_{OP'}$	h'	$b_{OP'}$	h'
No-piloting cue	<u>25°</u>	<u>50°</u>	Not applicable	Not applicable	20° (0.48)	57° (0.67)
Displaced proximal landmark	25°	<u>50°</u>	<u>75°</u>	Undetermined	95° (0.48)	72° (0.79)
Rotated distal scene	25°	50°	Undetermined	<u>150°</u>	Undetermined	140° (0.71)
Rotated distal scene and instruction	<u>25°</u>	50°	Undetermined	<u>150°</u>	30° (0.48)	138° (0.75)

The predicted $b_{OP'}$'s and h 's consistent with the observed $b_{OP'}$'s and h 's are underlined

Fig. 3 Observed and predicted bearing from the origin to the estimated testing position ($b_{OP'}$) relative to the first street (from O to T). **a** No-piloting cue condition. **b** Displaced proximal landmark condition. **c** Rotated distal scene condition. **d** Rotated distal scene and instruction condition. Each blue dot indicates one observed $b_{OP'}$ of one path of one participant. (The signs of $b_{OP'}$ for the left-turning path are flipped.) The solid black line indicates the circular mean observed $b_{OP'}$. The black arc indicates the 95% circular confidence interval of the mean observed $b_{OP'}$. The red arc indicates no reliable confidence interval of the mean observed $b_{OP'}$. The dotted red line indicates the predicted $b_{OP'}$ following self-motion cues (25°). The dashed green line indicates the predicted $b_{OP'}$ following the proximal landmark (75°) in the displaced proximal landmark condition (**b**)

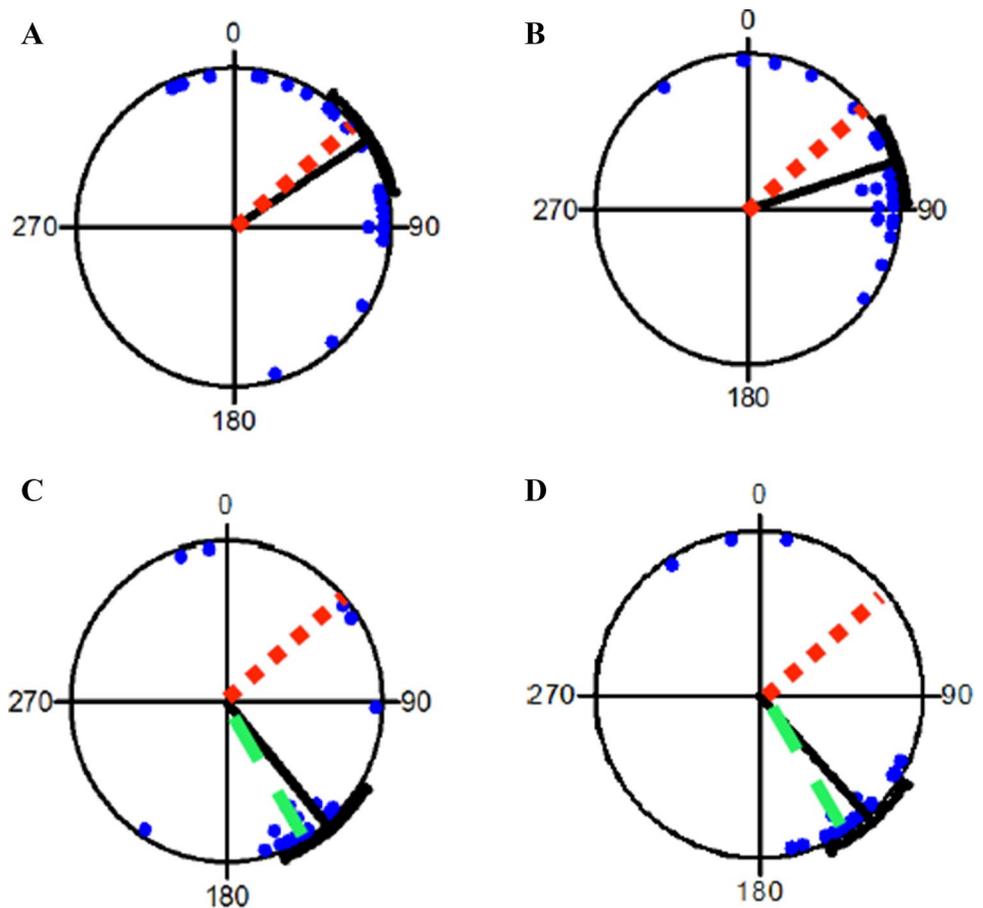


summarize all of these predicted values from different cues in Table 3.

We used the 95% circular confidence interval (CI) of the mean direction (of the 24 $b_{OP'}$ and 24 h') in each cue condition calculated by the circular statistic software Oriana 4 (Kovach Computing Services, UK) to diagnose the cues that determined $b_{OP'}$ and h' (Batschelet 1981). For example, if the confidence interval of an observed mean direction (e.g., $b_{OP'}$) includes the direction predicted by cue A, then it suggests that the observed direction is based on cue A. When

the confidence interval is not reliable because the combination of concentration of observed directions and the sample size is low, we will conclude that the estimated direction is undetermined. The Rayleigh test is widely used to test the null hypothesis that observed directions are uniform when we do not know the alternative direction. According to Batschelet, the confidence interval test is more appropriate than the Rayleigh test in the current study as we have specific directions (e.g., predicted by self-motion cues) as an alternative to the null hypothesis of uniform directions. We have

Fig. 4 Observed and predicted testing headings (h') relative to the first street (from O to T). **a** No-piloting cue condition. **b** Displaced proximal landmark condition. **c** Rotated distal scene condition. **d** Rotated distal scene and instruction condition. Each blue dot indicates one observed h' of one path of one participant (the signs of h' for the left-turning path are converted by flipping the sign). The solid black line indicates the circular mean observed h' . The black arc indicates the 95% circular confidence interval of the mean observed h' . The dotted red line indicates the predicted h' following self-motion cues (50°). The dashed green line indicates the predicted h' following the rotated distal scenes (150°) in the rotated distal scene condition and in the rotated distal scene and instruction condition (c, d)



still reported the results of the Rayleigh test for readers who may be interested.

Results and discussion

In the no-piloting cue condition, participants used self-motion cues to estimate their positions (Fig. 3a) and headings (Fig. 4a) [mean $b_{OP'}$ = 20° , 95% CI (348° – 52°) mean h' = 57° , 95% CI (36° – 78°)]. The confidence intervals included the predictions from self-motion cues for both $b_{OP'}$ and h' , 25° and 50° , respectively. The observed means of $b_{OP'}$ and the predicted means of $b_{OP'}$ based on self-motion cues were consistent. This finding indicates that participants were able to update the representations of their positions and headings using self-motion cues. It also confirms the validity of the least squares fitting method that calculated the observed position and heading estimations.

In the displaced proximal landmark condition, the estimated positions (Fig. 3b) followed the displaced tower [mean $b_{OP'}$ = 95° , 95% CI (63° – 126°)]. The confidence interval included the prediction from the landmark (75°) but excluded the prediction from self-motion cues (25°). The estimated headings (Fig. 4b) were close to what was predicted by self-motion cues [mean h' = 72° , 95% CI

(57° – 87°)]. The confidence interval excluded the prediction from self-motion cues (50°), although the lower boundary was close to the prediction.

In the rotated distal scene condition, critically, participants' position estimations (Fig. 3c) were undetermined, as there was no reliable confidence interval for $b_{OP'}$. The estimated headings (Fig. 4c) followed the rotated distal scenes [mean h' = 140° , 95% CI (121° – 159°)]. The confidence interval included the prediction from the landmark (150°) but excluded the prediction from self-motion cues (50°).

In addition, the Rayleigh test showed that observed headings (h') were not uniform in any of the three conditions, Rayleigh $Z_s \geq 10.83$, $p < .001$. The observed bearings of estimated positions ($b_{OP'}$) were also not uniform in any of the three conditions, Rayleigh $Z_s \geq 3.00$, $p \leq .05$. Note that although the result of the Rayleigh test rejected the uniform distribution of $b_{OP'}$ in the rotated distal scene condition ($p = .05$), we still could not determine the direction of $b_{OP'}$ as there was no reliable confidence interval.

Most of these findings were consistent with the selective resetting hypothesis, which was based on the findings when participants walked in a small space. One important exception was that when participants saw rotated distal scenes, their position estimations were undetermined in the current

experiment, which is inconsistent with the prediction that participants' position estimations followed self-motion cues when they saw rotated distal landmarks (Mou and Zhang 2014). However, this finding can be explained by the locomotion-dependent selective resetting hypothesis. According to this hypothesis, when people drive in a large-scale environment, path integration updates heading estimates dynamically, but updates position estimates only when required.³ As discussed in the Introduction, path integration updates position representations only when required because estimating positions while driving is a challenge. As a result, in the current experiment, position representations in path integration had not been updated when participants saw the rotated distal scenes which further interrupted the possible position estimation when required. Thus participants' position estimations did not follow self-motion cues and were undetermined.

To further test this conjecture, Experiment 2 modified the rotated distal scene condition. Participants were instructed to keep track of the origin of the path (*O*) while driving (He and McNamara 2017; Wiener et al. 2011). In addition, after driving, they were asked to point to the origin of the path before the rotated distal scenes were presented. We assume that people use both position and heading representations to estimate the origin of the path (Mou and Zhang 2014). Thus, participants had to update their position estimates before pointing to the origin. As a result, this instruction forced them to produce their position representation using self-motion cues before they saw the rotated distal scenes. Therefore, their position estimations would follow self-motion cues.

Experiment 2

Method

Participants

Twelve university students (six men and six women) participated in the experiment to fulfill a partial requirement for an introductory psychology course. Before the experiment, all participants signed the consent form approved by the University of Alberta Research Ethics Board. Twelve

³ Continuous updating or updating only when required of positions could not be diagnosed by the results in the no-piloting cue condition. Because there was no conflicting heading cue to interrupt position estimation from path integration at the end of the outbound path, participants could still use the moving distances and turning angle from self-motion cues to calculate their positions, even if they updated positions only when required.

participants were tested following the number of participants used in each cue condition of Experiment 1.

Design and procedure

This experiment used the rotated distal scene condition in Experiment 1, with two modifications. First, participants were instructed to keep track of the origin of the path while driving. Second, when participants finished driving in the testing position, they were asked to point to the origin before viewing the rotated distal scenes. We termed this condition the rotated distal scene and instruction condition.

Results and discussion

Consistent with our conjectures, the participants' position estimations (Fig. 3d) followed self-motion cues [mean b_{OP} = 30°, 95% CI (35°–62°)]. The confidence interval included the prediction from self-motion cues (25°). As in Experiment 1, participants' heading estimations (Fig. 4d) followed the rotated distal scenes [mean h' = 138°, 95% CI (121°–156°)]. The confidence interval included the prediction from the landmark (150°) but excluded the prediction from self-motion cues (50°). In addition, the Rayleigh test showed that observed headings (h') were not uniform, Rayleigh Z_s = 13.45, p < .001, and the observed bearings of estimated positions (b_{OP}) were not uniform, Rayleigh Z_s = 5.56, p < .01.

General discussion

There are two important findings in the current study. First, when the proximal landmark (i.e., tower) reappeared at the testing position, participants' position estimations followed the displaced proximal landmark. When the distal scenes reappeared with a 100° rotation, participants' heading estimations followed the rotated distal scenes. Second, when the displaced proximal landmark reappeared, participants' heading estimations followed self-motion cues. When the rotated distal scenes reappeared, the participants' position estimations depended on whether participants were instructed to keep track of the origin of the path during locomotion. In particular, their position estimations followed self-motion cues with such instruction but were undetermined without such instruction.

The current findings significantly strengthen the selective resetting hypothesis. The results, together with the previous studies (Mou and Zhang 2014; Zhang and Mou 2017), indicate that regardless of the travelling modes (walking or driving) and the scale (small or large) of the environment, a displaced proximal landmark determines people's position estimations, whereas rotated distal scenes determine their

heading estimations. These findings suggest that different piloting cues (i.e., heading cues or position cues) selectively reset the headings or positions estimated by path integration.

However, one finding in the current study strikingly differed from those in Mou and Zhang's (2014) study and questioned the selective resetting hypothesis. In Mou and Zhang's study, when rotated distal cues reappeared, participants' position estimations followed self-motion cues (2014). By contrast, in Experiment 1 of the current study, when rotated distal scenes reappeared, participants' position estimations appeared to be random (undetermined). This novel finding undermined one important claim of the selective resetting hypothesis. According to the selective resetting hypothesis, path integration dynamically updated participants' position representations as well as their heading representations. Therefore, both position and heading representations should have been updated in path integration before the rotated distal landmarks reappeared. As a consequence, participants' position estimations should have followed self-motion cues regardless of the locomotion mode. These predictions are inconsistent with the findings in Experiment 1.

The locomotion-dependent resetting hypothesis, however, could explain the discrepancy in Mou and Zhang's findings (2014) and in Experiment 1 of the current study. According to this hypothesis, when people walk, path integration updates their position and heading representations continuously. In contrast, when people drive, path integration updates their heading representations continuously, but updates their position representations only when participants are required to do so. This difference occurs because updating position representations is more complex than updating heading representations. One possible reason is that calculating position representations requires the input of heading representations, but not vice versa. The complexity in updating position representations, relative to updating heading representations, might be unnoticeable when people walk but might be significant when people drive. Historically, humans have much more experience walking than driving. Furthermore, walking provides people with richer idiothetic cues than driving does. In addition, walking is much slower than driving. Therefore, it makes sense that position representations would be updated continuously for walking but only when required for driving. In particular, when the rotated distal landmark reappeared, participants in Mou and Zhang's study had obtained position representations in path integration, whereas participants in Experiment 1 of the current study had not produced position representations in path integration. We assumed that seeing the rotated distal landmark interrupted the process of calculating positions when participants were required to do position estimation. That is why participants' position estimations followed self-motion cues in Mou and Zhang's study but did not follow

self-motion cues and were undetermined in Experiment 1 of the current study.

The speculation that the random (i.e., undetermined) position estimations in the rotated distal scene condition of Experiment 1 resulted from updating of position representations only when required was further supported in Experiment 2 of the current study. In Experiment 2, participants were instructed to keep track of the origin of the path (He and McNamara 2017; Wiener et al. 2011). The result showed that participants' position estimations followed self-motion cues when the rotated distal scenes reappeared, replicating the findings in Mou and Zhang's (2014) study. As discussed in the introduction, people need to know their positions and headings before they estimate their home locations. That explains why, in Experiment 2, participants updated their position estimations when they kept track of the origin of the path while driving. Path integration had produced the position estimation before the rotated distal scene reappeared. Thus, the participants' position estimations followed self-motion cues.

Although the rotated distal landmark led to random (undetermined) position estimates, the displaced proximal landmark did not lead to random heading estimates while driving. The locomotion-dependent resetting hypothesis provides an explanation. According to this hypothesis, path integration updates heading representations continuously whether people drive or walk. In the current study, heading representations in path integration had been updated before the displaced proximal landmark reappeared. Consequently, participants' heading estimations followed self-motion cues.

We acknowledge that the two kinds of updating (continuous updating and updating only when required) distinguished in the locomotion-dependent resetting hypothesis were inspired by the idea that individuals can have two spatial updating mechanisms while walking (e.g., Loomis et al. 1999). According to Loomis et al. (1999), individuals could continuously update the homing vector during locomotion (continuous updating). Individuals could also maintain the shape of the path during locomotion. They calculate the homing vector at the end of the path (configural updating). Extending this original idea, the current study's findings suggest three new insights.

First, the two spatial updating mechanisms in the previous studies focus on whether the homing vector is calculated continuously or only when required (He and McNamara 2017; Wiener et al. 2011). By contrast, in the locomotion-dependent resetting hypothesis, the two spatial updating mechanisms focus on whether participants' positions are calculated continuously or only when required. In the current study, during the test, participants pointed to buildings. Their position estimations were calculated with their response with regard to the directions of the buildings. Participants' responses to the home location

were not collected or used to calculate their position estimations. As a consequence, participants should have updated their positions with respect to many locations in the environment rather than the home only. This suggests that updating (continuous or not) is about vectors between people's positions and several important locations in the environment. The homing vector might be just one of these vectors.

Second, the previous studies found that the two spatial updating mechanisms were selected by instruction. In Wiener et al.'s study (2011; see also He and McNamara 2017 and Experiment 2 of the current study), participants could be instructed to update only at the end of the outbound path (e.g., by paying attention to the shape of the path) or continuously during locomotion (e.g., by keeping track of the origin of the path). The current study further shows that two spatial updating mechanisms could be selected by the locomotion mode, as the locomotion-dependent resetting hypothesis suggests. Participants who walked updated positions continuously (Mou and Zhang 2014), whereas participants who drove updated positions only when required (Experiment 1 of the current study). There might be other ways to activate the two spatial updating mechanisms. Future studies may test whether the complexity of the outbound path can also activate these two updating mechanisms. For example, if participants walk on a more complicated path with more legs (e.g., Kelly et al. 2008), position estimations might also be updated only when required (Loomis et al. 1999).

Third, the previous theories hypothesized that people might represent the configuration (i.e., shape) of the path through the configural updating mechanism (e.g., Loomis et al. 1999; Wiener et al. 2011). However, the random position estimations in the rotated distal scenes condition in Experiment 1 indicated that at least while driving, the length of travel legs and the turning angle are still separately represented as a cognitive graph (Warren et al. 2017) and have not been integrated into an enduring representation of the path shape, a cognitive map (Loomis et al. 1999). If an enduring representation of the path shape has been formed, the rotated distal scene should not impair it. Thus, participants should be able to use the enduring representation of the path shape to calculate the position, producing a position estimation that is consistent with self-motion cues rather than a random position estimation as indicated by the result. In future studies, we may test whether participants who are instructed to form an enduring representation of a path shape will show random position estimations when they see a rotated distal scene like in the rotated distal scenes condition in Experiment 1. It is possible that being instructed to pay attention to the shape of the path (Wiener et al. 2011) while driving can lead to an enduring representation of the outbound path, which participants can use to calculate their positions even when they see the rotated distal landmark.

We acknowledge that the findings of the current study are based on navigation in immersive environments without constant coherence between inertial cues and visual cues. Participants in the current study, with a tracked HMD, could move their head to change their views during driving. Therefore, inertial cues and visual cues were coherent while the car was moving forward within streets. However, when the virtual car turned across streets, the visual information indicated the turn whereas inertial cues did not, disrupting the coherence between inertial cues and visual cues. Thus, although driving a virtual car in an immersive virtual environment added some inertial cues compared to driving in a non-immersive virtual environment (e.g., tele-operating a vehicle or a drone), it was still not the same as driving in real environments. Previous studies showed that humans recalibrated the inertial information in terms of the visual information when the relations between inertial and visual cues changed systematically (e.g., Viaud-Delmon et al. 1998). In addition, hamsters relied less on inertial information in homing when both inertial and visual information were available even after they had briefly been rotated on a rotating platform in darkness (Etienne et al. 1990). These findings suggest that human and non-human animals are very sensitive to incoherence between inertial and visual information. We speculate that participants while driving across streets relied on the visual turning angle less the turning angle from their inertial cues to calculate the turning angles as participants in the No-piloting cue condition were accurately in estimating their headings. Future studies may test the locomotion-dependent selective resetting hypothesis in a driving stimulator providing constantly coherent inertial cues to understand resetting in real-life driving.

Conclusion

In conclusion, when people drive in a large-scale immersive virtual environment, the rotated distal scenes and the displaced proximal landmark selectively reset the heading and position estimations. Path integration uses self-motion cues to update position and heading estimates. Heading updating is continuous, but position updating may require more cognitive effort to work continuously. These results, together with the findings in previous studies (Mou and Zhang 2014; Zhang and Mou 2017), support the locomotion-dependent selective resetting hypothesis.

Acknowledgements This work was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC), Canada to Weimin Mou.

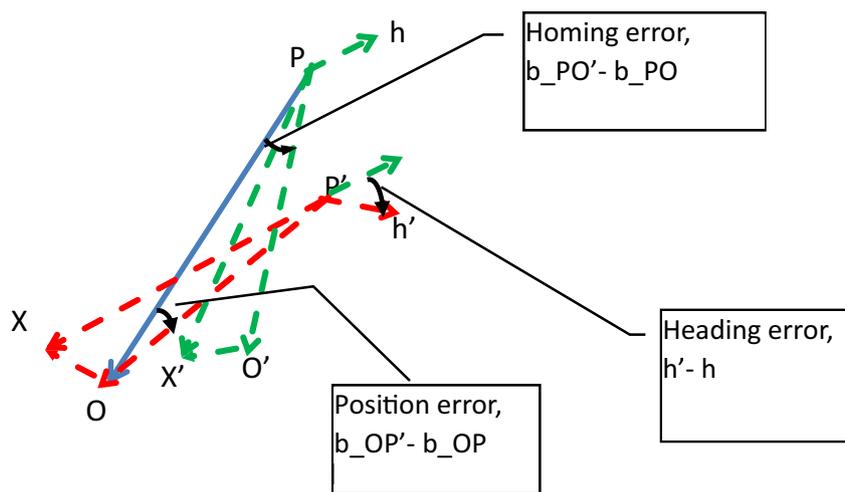


Fig. 5 A hypothetic participant while standing at the testing position (P) with the testing heading (h) points to the location of the origin (O). Suppose that the judged location of O is O' . The angular error of homing is $b_{PO'} - b_{PO}$. b_{AB} refers to a bearing from positions A to B relative to an horizontal allocentric reference direction in the environment. Suppose that this participant's estimates of his or her testing position and heading are P' and h' . The angular error of heading is $h' - h$. Both h and h' are specified by the angular distance from the allocentric reference direction. The angular error of posi-

tion is $b_{OP'} - b_{OP}$. As derived in the “Appendix”, homing error = position error – heading error. Position errors and heading errors cannot be dissociated with the measured homing errors. If this participant also learns an addition location X and then replaces X in the position of X' , then position errors can be measured by $(b_{OX} - b_{PO}) - (b_{O'X'} - b_{PO'})$ [see Mou and Zhang (2014) for derivation] and heading errors can also be measured given the measured position errors and homing errors (heading error = position error – homing error)

Appendix

Derivation of homing error = position error – heading error (i.e., $b_{PO'} - b_{PO} = (b_{OP'} - b_{OP}) - (h' - h)$) (see Fig. 5).

We assume that this participant uses the represented spatial relations between the origin (O), the estimated testing position (P'), and the estimated testing heading (h') in his or her spatial memory to judge the relations between replaced location of the origin (O'), the testing position (P), and the testing heading (h) during response. Hence the relations between the elements in the memory (O, P', h') should be the same as the relations between the elements in the response (O', P, h).

We obtain

$$h' - b_{OP'} = h - b_{O'P} \tag{1}$$

All headings (h and h') and bearings (i.e., b_{AB}) are defined as the angular distance from a fixed allocentric direction in the environment. We further define the clockwise direction as the positive direction to specify an angular distance. As signed angles belong to real numbers, all the mathematical principles for real numbers should be applied to headings and bearings.

Equation 1 can be rewritten as

$$h' - h = b_{OP'} - b_{O'P} \tag{2}$$

Therefore,

$$\begin{aligned} b_{OP'} - b_{OP} - (h' - h) &= b_{OP'} - b_{OP} \\ &- (b_{OP'} - b_{O'P}) \\ &= b_{O'P} - b_{OP} \end{aligned}$$

We obtain

$$b_{OP'} - b_{OP} - (h' - h) = b_{O'P} - b_{OP} \tag{3}$$

Because $b_{AB} = b_{BA} - 180$, we rewrite Eq. 3 as

$$\begin{aligned} b_{OP'} - b_{OP} - (h' - h) &= b_{PO'} - 180 - (b_{PO} - 180) \\ &= b_{PO'} - b_{PO}. \end{aligned}$$

We obtain

$$b_{PO'} - b_{PO} = b_{OP'} - b_{OP} - (h' - h) \text{ or homing error} = \text{position error} - \text{heading error}.$$

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