Cognition 133 (2014) 553–571

Contents lists available at ScienceDirect

Cognition

journal homepage: www.elsevier.com/locate/COGNIT

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

Weimin Mou *, Lei Zhang

University of Alberta, Canada

ARTICLE INFO

Article history:
Received 7 January 2014
Revised 13 August 2014
Accepted 14 August 2014
Available online 14 September 2014

Keywords:
Position estimation
Heading estimation
Path integration
Reference direction
Idiothetic cues
Allothetic cues

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

* Corresponding author. Address: Department of Psychology, P217 Biological Sciences Bldg, University of Alberta, Edmonton, Alberta T6G 2E9, Canada.

E-mail address: wmou@ualberta.ca (W. Mou).

http://dx.doi.org/10.1016/j.cognition.2014.08.010
0010-0277/

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.