Effects of Target Preview on Path Integration: Postprint

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Abstract

This study utilized head-mounted virtual reality and path completion tasks that involved returning to the origin or to landmarks, manipulating participants'prior knowledge of the return location through instructional cues to investigate the effect of target prior knowledge on human path integration. The experimental results indicate that prior knowledge of returning to the origin enables participants to effectively ignore interference resulting from landmark appearance or increased landmark quantity, whereas greater prior knowledge of returning to a landmark promotes more accurate responses. These findings demonstrate that target prior knowledge, as a non-perceptual factor, influences human path integration, and also reflect the strategic and flexible nature of human path integration.

Full Text

The Influence of Target Knowledge on Path Integration

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Abstract

Path integration refers to a navigation strategy in which navigators update their spatial relationship with the environment by integrating self-motion information. This study employed head-mounted virtual reality and a path completion task requiring participants to return to either the origin or a landmark location. By manipulating participants' foreknowledge of the return location through instructional cues, we examined how target knowledge influences human path integration. The results demonstrated that foreknowledge of returning to the origin enabled participants to effectively ignore interference caused by the presence or increased number of landmarks. Conversely, greater foreknowledge of returning to a landmark location promoted more accurate responses. These findings illustrate that target knowledge, as a non-perceptual factor, influences human path integration and highlight the strategic and flexible nature of human path integration.

Keywords: path integration; target knowledge; landmark; virtual reality; spatial navigation

Path integration is a navigation strategy in which navigators update their spatial relationship with the environment by integrating self-motion information. Research on path integration initially focused primarily on animal foraging behavior, particularly the phenomenon of desert ants returning directly to their nests after finding food by relying solely on self-motion information. Subsequent studies have measured path integration abilities in various species including geese, dogs, and rats (Wan, 2016). For humans, using self-motion information for path integration represents a crucial ability for updating spatial relationships with the environment, especially when environmental information is limited. The self-motion information that humans rely on for path integration can be categorized into endogenous and exogenous sources. Endogenous information includes proprioceptive and vestibular cues, whereas exogenous information includes optic flow. Human path integration can be based exclusively on endogenous information, exclusively on exogenous information, or on an integration of both (Guo & Wan, 2015; Kearns, Warren, Duchon, & Tarr, 2002; Loomis, Klatzky, Golledge, Cicinelli, Pellegrino, & Fry, 1993; Zhou & Zhang, 2005). The primary experimental paradigm used in human path integration research is the path completion task, also known as the return-to-origin task. This task requires participants to travel along an outbound path consisting of multiple segments from a starting point, reach the end of the path, and then return directly to the origin. Studies using virtual reality have shown that even for complex outbound paths (e.g., containing 12 segments), people can still update their spatial relationship with the origin to some extent (Wan, Wang, & Crowell, 2013).

Of course, spatial navigation in both animals and humans can also rely on landmark information (Collett & Graham, 2004; Foo, Warren, Duchon, & Tarr, 2005; Li & Yang, 2015). Although path integration is defined as relying exclusively on self-motion information while excluding landmarks, the presence of landmarks in path integration experiments can influence human performance. For example, if participants preview landmarks along the path or memorize landmark information beforehand, their performance in subsequent path completion tasks improves (Philbeck, Klatzky, Behrmann, Loomis, & Goodridge, 2001; Philbeck & O' Leary, 2005). When information from path integration and landmarks conflicts, competition occurs between the two systems (Zhang & Mou, 2017), and the stability of landmarks affects how people weigh and use landmark information versus path integration (Zhao & Warren, 2015). When landmark information is clear and stable, people may rely more heavily on landmarks during spatial navigation (Foo, Duchon, Warren, & Tarr, 2007), whereas path integration occurs primarily in environments where only self-motion information is available (e.g., Poucet, Sargolini, Song, Hangya, Fox, & Muller, 2014). When landmark information is ambiguous, people acquire survey knowledge about the environment through path integration (Foo, Warren, Duchon, & Tarr, 2005). Cheng, Shettleworth, Huttenlocher, and Riese (2007) proposed that path integration serves as a "back-up and reference system" in animal spatial navigation. Specifically, animals prefer to use other cues such as landmarks when conditions permit, but can resort to path integration when other cues become unreliable, and path integration helps animals detect whether landmarks and other cues are trustworthy and usable. For human path integration, Wang (2016) proposed the path integration-cognitive map hypothesis, suggesting that humans can obtain a dynamic cognitive map of the environment by performing spatial updating of multiple locations through multiple independent path integrations. In this process, landmark information can be used by navigators to reset or calibrate the path integration system (Sjolund, Kelly, & McNamara, 2018; Zhang & Mou, 2017). In summary, path integration and landmark learning are interdependent and work together to provide navigators with a coherent spatial representation.

What cognitive factors might influence the relationship between landmarks and path integration? Knowledge about the target location may be an important factor. Wan, Wang, and Crowell (2012) investigated the effect of landmarks on path integration by modifying the typical return-to-origin task. They used a return-to-origin-or-landmark task in which two landmarks were placed at specific locations (i.e., intersections between path segments) along the outbound path. Under different experimental conditions, participants were asked to return directly to either the origin or a landmark location upon reaching the end of the outbound path. Participants were divided into two groups: an "informed" group and an "uninformed" group. The informed group knew before the experiment began whether landmarks would be present along the outbound path and which location they would be asked to return to, allowing them to attend only to the relevant target while ignoring other locations. The uninformed group did not know which location they would be asked to return to, but they were told whether landmarks would be present. Therefore, when landmarks were present along the outbound path, they needed to pay attention to both the origin and all landmark locations. The results showed that regardless of whether participants were asked to return to the origin or a landmark location, response times were longer for the uninformed group than for the informed group. Moreover, the uninformed group showed longer response times when landmarks were present than when they were absent, whereas the informed group did not exhibit this effect.

Both egocentric representation with continuous updating and allocentric representation with configural updating can support path integration (He & McNamara, 2018; Wiener, Berthoz, & Wolbers, 2011). However, foreknowledge of the return location may allow participants to adopt flexible strategies. When they know the specific return target, they only need to update that single target (whether through continuous or configural updating). When they do not know the return target, they need to update all possible target locations. However, because the uninformed group also knew beforehand whether each trial included landmarks, they could form some expectations about the return target. In particular, when they knew in advance that a trial contained no landmarks, they could infer that the task required returning to the origin.

To systematically examine how target knowledge influences path integration, the present study adopted the return-to-origin-or-landmark task from Wan et al. (2012) and manipulated the number of landmarks by adapting the method used by Wang et al. (2006) to study the effect of object quantity. We systematically manipulated participants' foreknowledge of the return location (target) through instructional cues to investigate its influence on path integration. The study included trials with no landmarks, one landmark, or two landmarks. This experimental design allowed us to distinguish three levels of target knowledge: (1) complete ignorance—no knowledge of landmark presence or return location before the trial; (2) return-type knowledge—knowledge of landmark presence and whether to return to the origin or a landmark (but not which specific landmark); and (3) return-location knowledge—knowledge of landmark presence and which specific location to return to. The degree of target knowledge increased progressively from complete ignorance to return-type knowledge to return-location knowledge.

We predicted that when asked to return to the origin, the complete ignorance group' s performance would be affected by landmarks (presence and number), whereas the other two groups, knowing from the outset that they would be asked to return to the origin, would not show such effects. When asked to return to a landmark, performance would improve with increasing target knowledge, with the complete ignorance group showing the worst performance, the return-type knowledge group showing intermediate performance, and the return-location knowledge group showing the best performance.

2.1 Participants

Forty-eight undergraduate students from Tsinghua University (24 male, 24 female) participated in the study. Their ages ranged from 18 to 22 years (M = 19.6, SD = 1.0). All had normal or corrected-to-normal vision and no color blindness or color weakness. Participants received either course credit for a psychology elective or 30 RMB as compensation. Using G*Power 3.1.9.3 software, we estimated the required sample size with an expected effect size of 0.25 and statistical power of 1 - $\beta = 0.9$, which yielded a recommended total sample of 45 participants. The planned sample size was thus consistent with the actual sample size.

2.2 Apparatus and Materials

This study used the nVisor SX60 head-mounted virtual reality device from Worldviz, with a display refresh rate of 60 Hz and a field of view of 44° (horizontal) × 34° (vertical). The response device was a Logitech F710 wireless gamepad, with three buttons used as response keys for walking, rotational responses, and distance responses. The virtual reality scenes were created using 3D Max software, and experimental control and data recording were implemented through Vizard 4.0 software.

The outbound path in the path completion task consisted of five virtual corridors (as shown in [Figure 1: see original paper]). Each corridor segment was either 3 m or 5 m long, 2.2 m high, and 1 m wide. The walls, floor, and ceiling were textured with gray rock. The angle between any two consecutive corridors was either 60° or 120°. The length of each corridor segment, the magnitude and direction (clockwise or counterclockwise) of the angle between any two segments were randomly determined under the constraint that no two non-consecutive segments intersected. The outbound path could contain zero, one, or two landmarks. The possible landmarks were a red triangle or a blue square. Since participants could not see landmarks when positioned at the end of the outbound path, landmarks could only appear at the ends of the first, second, or third corridor segments. When only one landmark was present in the outbound path, which landmark appeared and its location were randomly determined by the computer. When two landmarks were present, the location of each landmark was also randomly determined by the computer. When participants reached the end of the outbound path, they found themselves in a circular room with a radius of 0.5 m and a height of 2.2 m. The surface texture changed to yellow rock, signaling that they had reached the endpoint. At this point, a blue indicator rod appeared, extending from the participant' s body to the wall of the circular room and parallel to the ground. The rod rotated with the participant' s body, indicating their facing direction. Simultaneously, a shape appeared in front of the participant, indicating which location they should return to. Specifically, a purple circle indicated returning to the origin, while a red triangle or blue square indicated returning to the corresponding landmark location. After participants made their directional response, a 1000 m long corridor appeared in the direction they had chosen for them to make their distance response. This corridor was 2.2 m high and 1 m wide, with a yellow rock texture.

In the virtual environment of this study, participants' linear walking was accomplished through "virtual" walking by pressing a button while keeping their body stationary. They perceived movement distance only through optic flow information, and the movement speed was set at a constant 1.5 m/s. However, when turning at corridor corners or making directional responses, participants physically rotated their bodies, thus perceiving rotation through both optic flow and proprioceptive information.

2.3 Experimental Design

This study employed a 3 (target knowledge) × 3 (number of landmarks: 0, 1, 2) mixed design, with target knowledge as a between-subjects variable and number of landmarks as a within-subjects variable. Before the experiment, participants were randomly assigned to three groups of 16 participants each and received different instructions at the beginning of each trial, resulting in progressively increasing levels of target knowledge. The first group received no information about whether landmarks would be present in the outbound path or which location they would be asked to return to; this was the complete ignorance group. The second group was told before each trial whether landmarks would be present and whether they would be asked to return to the origin or a landmark; this was the return-type knowledge group. The third group was told before each trial whether landmarks would be present and which specific location (origin or which landmark) they would be asked to return to; this was the return-location knowledge group. Notably, even when participants were told that landmarks would be present in the upcoming trial, they did not know whether there would be one or two landmarks.

Each participant completed 24 trials of the path completion task, including 8 trials with no landmarks, 8 trials with one landmark, and 8 trials with two landmarks. In trials without landmarks, participants always returned to the origin. In trials with landmarks, half required returning to the origin and half required returning to a landmark location. When two landmarks were present, the probability of returning to each landmark was equal. Thus, the experiment included five different task conditions: (1) no landmark, return to origin (as shown in [Figure 2: see original paper]A); (2) one landmark in the outbound path, return to origin (as shown in [Figure 2: see original paper]B); (3) one landmark in the outbound path, return to landmark (as shown in [Figure 2: see original paper]C); (4) two landmarks in the outbound path, return to origin (as shown in [Figure 2: see original paper]D); and (5) two landmarks in the outbound path, return to one of the landmarks (as shown in [Figure 2: see original paper]E).

2.4 Experimental Procedure

First, participants read prepared instructions and completed 4 to 8 practice trials until they felt they understood the task. They then proceeded to the formal experiment consisting of 24 trials. Before each trial, participants in different groups received different types of instructions. The ignorance group received the instruction: "A new trial begins." The return-type knowledge group received: "A new trial begins; this trial requires returning to the origin/landmark." The return-location knowledge group received: "A new trial begins; this trial requires returning to the origin/triangle landmark/square landmark."

At the start of each trial, participants appeared at the beginning of the first corridor segment, facing the end of that segment (see [Figure 1: see original paper]A). They pressed the walking key to "virtually" walk to the end of the corridor. Upon reaching the end, the next corridor segment appeared. Because there were angles between corridors, participants needed to rotate their bodies to face the end of the next corridor segment before continuing to walk (see [Figure 1: see original paper]B). After traversing all five corridor segments, participants entered a circular room with yellow rock walls. Simultaneously, the indicator rod showing their body orientation and the shape indicating the return location appeared (see [Figure 1: see original paper]C), informing participants which location to return to in that trial. Participants then rotated their body to face the target location and pressed the direction confirmation key. Their response angle and response time were recorded by the computer. In the direction they had chosen, a long corridor appeared (see [Figure 1: see original paper]D), and participants walked a distance by pressing the walking key. When they felt they had reached the return location, they pressed the position confirmation key. Their distance response was then recorded, the trial ended, and the next trial began. Throughout the entire experiment (including practice trials), participants received no feedback.

Of the 48 participants, 47 completed all 24 trials; one participant completed only 21 trials due to technical failure and was included in the data analysis. However, because some participants occasionally made key-press errors in certain trials and failed to respond with direction or distance, we excluded trials with a response distance of 0 or directional responses between 0° and 3° from the data analysis. These excluded trials accounted for 4.1% of the total trials. Participants' path integration performance was measured using two indicators: position error and response time. Response time in this study measured the time taken to make the directional response, while position error referred to the distance between the location where participants stopped and the actual target location.

First, we conducted a 3 (group: complete ignorance, return-type knowledge, return-location knowledge) × 3 (number of landmarks: 0, 1, 2) mixed-design ANOVA on the position error and response time data for return-to-origin trials shown in [Figure 3: see original paper], with group as a between-subjects variable and number of landmarks as a within-subjects variable. The results showed that except for a significant interaction between group and number of landmarks on response time, $F(4, 90) = 2.54$, $p = 0.045$, $p^2 = 0.10$, no other main effects or interactions were significant, all $Fs < 1.96$, $ps > 0.13$. To interpret this interaction, we conducted pairwise comparisons of response times for each group across different landmark numbers. The results indicated that the complete ignorance group showed significantly longer response times when returning to the origin with two landmarks (10.63 s) than with no landmarks (8.48 s), $t(15) = 3.49$, $p < 0.01$, Cohen's $d = 0.97$. However, neither of these conditions differed significantly from the response time with one landmark (11.19 s), both $ts < 1.52$, $ps > 0.45$. The other two groups showed no such effects, all $ts < 1.76$, $ps > 0.30$. *All pairwise comparisons reported here and below were Bonferroni-corrected, and p-values reported in the text are corrected values.

Next, we conducted a 3 (group: complete ignorance, return-type knowledge, return-location knowledge) × 2 (number of landmarks: 1, 2) mixed-design ANOVA on the position error and response time data for return-to-landmark trials shown in [Figure 4: see original paper], with group as a between-subjects variable and number of landmarks as a within-subjects variable. It should be noted that when no landmarks were present in the outbound path, there was no return-to-landmark condition; therefore, the number of landmarks could only be 1 or 2. The ANOVA results showed a significant main effect of group on position error, $F(2, 45) = 4.49$, $p = 0.017$, $p^2 = 0.17$. Multiple comparisons revealed that the complete ignorance group showed significantly greater position error (13.48 m) than the return-type knowledge group (10.66 m), $t(30) = 2.24$, $p = 0.049$, Cohen' s $d = 0.58$, and also significantly greater error than the return-location knowledge group (10.44 m), $t(30) = 2.46$, $p = 0.043$, Cohen' s $d = 0.91$. The difference between the return-type knowledge and return-location knowledge groups was not significant, $t(30) = 0.26$, $p > 0.99$. Additionally, the interaction between group and number of landmarks on response time was significant, $F(2, 45) = 5.23$, $p = 0.009$, $p^2 = 0.19$. One-way ANOVAs on response time for each group showed that response times for the complete ignorance and return-type knowledge groups were not affected by the number of landmarks, both $Fs < 2.30$, $p > 0.14$. However, the return-location knowledge group showed even shorter response times when returning to the origin with two landmarks (7.71 s) than with one landmark (8.48 s), $F(1, 15) = 8.13$, $p = 0.012$, $p^2 = 0.35$.

4.1 The Influence of Target Knowledge on Path Integration

The results of this study indicate that target knowledge facilitates both return-to-origin and return-to-landmark responses, though the specific mechanisms differ. On one hand, the influence of target knowledge on return-to-origin responses is primarily manifested in its interaction with the number of landmarks. Specifically, when the task required returning to the origin, the complete ignorance group showed longer response times with two landmarks than with no landmarks, whereas the return-type knowledge and return-location knowledge groups showed no such effects. These findings align with our predictions and demonstrate that foreknowledge of returning to the origin enables participants to effectively ignore interference caused by the presence or increased number of landmarks. On the other hand, when the task required returning to a landmark, both the return-type knowledge and return-location knowledge groups showed smaller position errors than the complete ignorance group, suggesting that greater foreknowledge of returning to a landmark promotes more accurate responses.

The facilitative effect of target knowledge on path integration may be attributed to participants adopting more adaptive strategies based on knowledge of the return location. For example, the complete ignorance group needed to update their spatial position from the very beginning of the outbound path, resulting in more errors. The return-type knowledge group could begin spatial updating only from when landmarks appeared, and the return-location knowledge group could even begin updating only from when they knew which specific landmark they needed to return to. These two groups could ignore the path segments before the target, reducing the working memory load imposed by the task and simplifying their processing of the outbound path. As described in the Method section, since landmarks could only appear at the ends of the first, second, or third corridor segments, these two groups could simplify the outbound path they needed to cognitively process to include only two, three, or four segments.

Thus, this study also demonstrates the importance of working memory for path integration by revealing participants' efforts to reduce working memory load. Whether returning to the origin or a landmark, path integration requires simultaneous processing of distance and direction information, and position error is influenced by both direction error and distance error. Chrastil et al. (2016) found that the hippocampus, retrosplenial cortex, and parahippocampal gyrus are responsible for encoding and maintaining path integration information in working memory. The hippocampus, retrosplenial cortex, and parahippocampal gyrus are critical for processing distance information in path integration, while the retrosplenial cortex is also important for processing direction information. Neural evidence suggests that the processing of distance and direction information in path integration may involve dissociable mechanisms in working memory. Moreover, the role of working memory in path integration may show substantial individual differences (Arnold, Burles, Bray, Levy, & Iaria, 2014). This study reflects the influence of working memory on path integration at the behavioral level and reveals the flexible strategies individuals may adopt to reduce working memory load during path integration.

4.2 The Influence of Target Knowledge on Spatial Navigation

The findings of this study further illuminate the relationship between landmark-based navigation and path integration based on internal cues. By operational definition, path integration relies exclusively on self-motion information, with landmark influences strictly excluded. However, outside of tightly controlled experimental conditions, spatial navigation generally has access to both external cues such as landmarks and internal cues from self-motion. When both types of information are available, people rely more on clear and reliable landmark information (Foo et al., 2007) or integrate information from both strategies (Zhao & Warren, 2015). The present study adopted Wan et al.' s (2012) return-to-origin-or-landmark task paradigm, which increased the task relevance of landmarks for path integration. Although the origin of the outbound path may be more salient and prominent than encountered landmarks, the possibility of being asked to return to a landmark made these landmarks not merely cues for spatial navigation but potential return targets themselves. Therefore, target knowledge may also guide participants' attention to different types of spatial cues in a top-down manner (Theeuwes, 2010). Path integration and landmark learning compete with yet depend on each other, providing people with a coherent spatial representation.

The results of this study also enhance our understanding of how target knowledge influences spatial navigation. Although the present study and Wan et al. (2012) used different types of virtual reality equipment, both studies consistently show that foreknowledge of the target helps participants perform better in path completion tasks. However, when considering the present findings alongside spatial learning literature, target knowledge appears to have different effects on path integration versus the acquisition of environment-based structural knowledge. Rossano and Reardon (1999) had participants perform a spatial learning task in a virtual campus environment and found that when participants had a specific goal during spatial learning (i.e., constantly trying to remember the location of a particular building while touring the virtual campus), they acquired less environmental structural knowledge than when they had no specific goal. Their results can be explained by cognitive load theory (Sweller, 1994; Sweller & Chandler, 1994). When participants have a clear and specific goal (e.g., always remembering a particular location on campus), they may adopt a means-end strategy, constantly trying to reduce the discrepancy between their current state and the goal at each step of the task. This process consumes substantial cognitive resources, leaving insufficient resources for other cognitive activities (such as acquiring environmental structural knowledge or building a cognitive map), resulting in the specific goal actually hindering the acquisition of environmental structural knowledge. Notably, those spatial learning tasks involved environments rich in visual and landmark information. In contrast, the path integration in the present study is based on estimating and integrating self-motion information. Therefore, when participants' foreknowledge about the target increases, they can adopt strategies better adapted to task demands, reducing their working memory load and simplifying their cognitive processing of the outbound path. Given the difficulties and challenges people experience with path integration (Wan, 2016), the facilitative effect of target knowledge is particularly valuable.

Of course, this study has certain limitations. First, because the task included at most two landmarks, the effect of increasing landmark number on cognitive load may not have been sufficiently pronounced. Additionally, because landmarks were always placed at the ends of corridor segments, this specific placement coincided with spatial information about the path nodes themselves. Second, the head-mounted virtual reality display used in this study provided less immersion and a smaller field of view than the virtual cube used by Wan et al. (2012), and these objective constraints made path integration more difficult in the present study. Therefore, caution is needed when generalizing the conclusions of this study to other contexts.

In summary, the results of this study demonstrate the facilitative effect of target knowledge on path integration. When landmarks may appear along the outbound path, participants' performance is influenced by foreknowledge of the target, regardless of whether they are asked to return to the origin or a landmark.

The findings also illustrate the influence of expectations on human path integration. Future research could explore how knowledge and expectations about task goals affect the types of spatial representations and updating strategies participants adopt and how they allocate cognitive processing resources. Such findings would help us further understand the contribution of non-perceptual factors to human path integration and reveal the strategic and flexible nature of human path integration.

References

Arnold, A. E., Burles, F., Bray, S., Levy, R. M., & Iaria, G. (2014). Differential neural network configuration during human path integration. *Frontiers in Human Neuroscience, 8*, 263: doi: 10.3389/fnhum.2014.00263.

Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. (2007). Bayesian integration of spatial integration. *Psychological Bulletin, 133*, 625-637.

Chrastil, E. R., Sherrill, K. R., Hasselmo, M. E., & Stern, C. E. (2016). Which way and how far? Tracking of translation and rotation information for human path integration. *Human Brain Mapping, 37*, 3636-3655.

Collett, T. S., & Graham, P. (2004). Animal navigation: path integration, visual landmarks and cognitive maps. *Current Biology, 14*(12), R475-R477.

Foo, P., Duchon, A., Warren, W. H., & Tarr, M. J. (2007). Humans do not switch between path knowledge and landmarks when learning a new environment. *Psychological Research, 71*(3), 240-251.

Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map-versus landmark-based navigation of novel shortcuts. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 31*(2), 195-215.

Guo, J., & Wan, X. (2015). The effect of learning in virtual path integration. *Acta Psychologica Sinica, 47*(6), 711-720.

He, Q., & McNamara, T. P. (2018). Spatial updating strategy affects the reference frame in path integration. *Psychonomic Bulletin & Review, 25*(3), 1073-1079.

Kearns, M. J., Warren, W. H., Duchon, A. P., & Tarr, M. J. (2002). Path integration from optic flow and body senses in a homing task. *Perception, 31*, 349-374.

Klatzky, R. L., Beall, A. C., Loomis, J. M., Golledge, R. G., & Philbeck, J. W. (1999). Human navigation ability: Tests of the encoding-error model of path integration. *Spatial Cognition and Computation, 1*(1), 31-65.

Li, D., & Yang, Z. (2015). Spatial navigation: The relationship between landmark learning and path integration. *Advances in Psychological Science, 23*(10), 1755-1762.

Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., Pellegrino, J. W., & Fry, P. A. (1993). Nonvisual navigation by blind and sighted: assessment of path integration ability. *Journal of Experimental Psychology: General, 122*(1), 73–91.

Philbeck, J. W., & O' Leary, S. (2005). Remembered landmarks enhance the precision of path integration. *Psicológica, 26*, 7–24.

Philbeck, J. W., Klatzky, R. L., Behrmann, M., Loomis, J. M., & Goodridge, J. (2001). Active control of locomotion facilitates nonvisual navigation. *Journal of Experimental Psychology: Human Perception and Performance, 27*(1), 141–153.

Poucet, B., Sargolini, F., Song, E. Y., Hangya, B., Fox, S., & Muller, R. U. (2014). Independence of landmark and self-motion-guided navigation: A different role for grid cells. *Philosophical Transactions of the Royal Society B: Biological Sciences, 369*(1635), 20130370.

Rossano, M. J., & Reardon, W. P. (1999). Goal specificity and the acquisition of survey knowledge. *Environment and Behavior, 31*(3), 395–412.

Sjolund, L. A., Kelly, J. W., & McNamara, T. P. (2018). Optimal combination of environmental cues and path integration during navigation. *Memory & Cognition, 46*, 89–99.

Sweller, J. (1994). Cognitive load theory, learning difficulty, and instructional design. *Learning and Instruction, 4*(4), 295–312.

Sweller, J., & Chandler, P. (1994). Why some material is difficult to learn. *Cognition and Instruction, 12*(3), 185–233.

Theeuwes, J. (2010). Top-down and bottom-up control of visual selection. *Acta Psychologica, 135*(2), 77–99.

Wan, X., Wang, R. F., & Crowell, J. A. (2012). The effect of landmarks in human path integration. *Acta Psychologica, 140*(1), 7–12.

Wan, X. (2016). *The phenomenon and mechanisms of path integration in humans.* Hangzhou: Zhejiang University Press.

Wan, X., Wang, R. F., & Crowell, J. A. (2013). Effects of basic path properties on human path integration. *Spatial Cognition & Computation, 13*, 79–101.

Wang, R. F. (2016). Building a cognitive map by assembling multiple path integration. *Psychonomic Bulletin & Review, 23*, 692–702.

Wang, R.F., Crowell, J. A., Simons, D. J., Irwin, D. E., Kramer, A. F., & Ambinder, M.S. et al. (2006). Spatial updating relies on an egocentric representation of space: Effects of the number of objects. *Psychonomic Bulletin & Review, 13*(2), 281–286.

Wiener, J. M., Berthoz, A., & Wolbers, T. (2011). Dissociable cognitive mechanisms underlying human path integration. *Experimental Brain Research, 208*, 61-71.

Zhang, L., & Mou, W. (2017). Piloting systems reset path integration systems during position estimation. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 43*(3), 472-491.

Zhao, M., & Warren, W. H. (2015b). How you get there from here: Integration of visual landmarks and path integration in human navigation. *Psychological Science, 26*, 915-924.

Zhou, J.S., & Zhang, K. (2005). Kinestheic, Irrelevant Motion and Path Integration. *Psychological Science, 28*(6), 1306-1308.

Note: Figure translations are in progress. See original paper for figures.