Dissociable cognitive mechanisms underlying human path integration

Jan M. Wiener · Alain Berthoz · Thomas Wolbers

Abstract Path integration is a fundamental mechanism of spatial navigation. In non-human species, it is assumed to be an online process in which a homing vector is updated continuously during an outward journey. In contrast, human path integration has been conceptualized as a configural process in which travelers store working memory representations of path segments, with the computation of a homing vector only occurring when required. To resolve this apparent discrepancy, we tested whether humans can employ different path integration strategies in the same task. Using a triangle completion paradigm, participants were instructed either to continuously update the start position during locomotion (continuous strategy) or to remember the shape of the outbound path and to calculate home vectors on basis of this representation (configural strategy). While overall homing accuracy was superior in the configural condition, participants were quicker to respond during continuous updating, strongly suggesting that homing vectors were computed online. Corroborating these findings, we observed reliable differences in head orientation during the outbound path: when participants applied the continuous updating strategy, the head deviated significantly from straight ahead in direction of the start place, which can be interpreted as a continuous motor expression of the homing vector. Head orientation—a novel online measure for path integration—can thus inform about the underlying updating mechanism already during locomotion. In addition to demonstrating that humans can employ different cognitive strategies during path integration, our two-systems view helps to resolve recent controversies regarding the role of the medial temporal lobe in human path integration.

Keywords Path integration · Cognitive strategies · Spatial cognition

J. M. Wiener and T. Wolbers contributed equally to this manuscript.

J. M. Wiener (✉)
Department of Psychology, Bournemouth University,
Poole House, Talbot Campus, Fern Barrow,
Poole, Dorset BH12 5BB, UK
e-mail: jwiener@bournemouth.ac.uk

J. M. Wiener · A. Berthoz
CNRS, Collège de France, 75005 Paris, France

T. Wolbers
Centre for Cognitive and Neural Systems,
University of Edinburgh, Edinburgh, UK

Introduction

Path integration, the ability to integrate perceived self-motion information over time, is a fundamental mechanism of spatial navigation. It allows for keeping track of changes in position and orientation, provides vector knowledge about places encountered during travel, and is thus assumed to play a key role in cognitive mapping (Gallistel 1990). Recent evidence from animal research, for example, suggests that path integration provides a scaffold for landmark learning (Müller and Wehner 2010). Specifically, path integration information is combined with landmark information when novel landmarks are encoded. Even though everyday navigation strongly relies on landmark information (e.g., Newman et al. 2007), path integration appears to be an automatic process in that any perceptually signaled self-motion updates the representation of current spatial location and orientation (May and Klatzky 2000). Path integration usually interacts with landmark-based navigation (for an overview, see Etienne and Jeffery 2004)

but becomes particularly important when vision is corrupted (Loomis et al. 1993) or when reliable landmark information is not available. In addition, by providing coarse estimates of one's current position, path integration allows for prospective coding, i.e. for predicting locations or landmarks that are to be encountered while navigating familiar environments (Ferbinteanu and Shapiro 2003).

For all animal species, path integration is described as a continuous updating process during which ego-motion is integrated to update the home vector—i.e. a working memory representation of the distance and direction to the start place of the excursion (Benhamou and Séguinot 1995; Etienne and Jeffery 2004). In contrast, human path integration has predominantly been described to depend on a configural updating process. Human path integration is often studied with the triangle completion task, in which blindfolded participants are led along two sides of a triangle. At the end of this outbound path, they are released and asked to complete the triangle by walking back to the starting point. According to the encoding error model (EEM; Fujita et al. 1993), the traveled path is divided into straight line segments that are remembered. Only when asked to start homing do participants generate a survey representation of the traveled path and compute the home vector on basis of this representation (for more recent applications, see: Péruch et al. 1997; Klatzky et al. 1999; May and Klatzky 2000, Mahmood et al. 2009). The fact that participants are able to retrace the outbound paths if required and that response times increase with increasing path complexity (e.g., Loomis et al. 1993) provide support for such a configural path integration strategy.

It is important to note that continuous and configural path integration strategies differ in two crucial aspects: during purely continuous updating ego-motion information is used to instantaneously update the home vector. Continuous path integration thus is an *online* process—i.e. the home vector is computed during navigation—that *does not require* forming a representation of the path traversed. The only representation required is the home vector itself. Configural strategies, in contrast, require that the path configuration is remembered; ego-motion information is integrated to judge the length of the single segments and the angle in-between. The home vector is computed only at the end of the path. Thus, configural path integration is an *offline* process that *does require* the formation of a working memory representation of the traversed path. That is, continuous and configural updating differ both in the timing of the home vector calculation and in their working memory demands.

Whereas human path integration has been described to rely on configural updating, there are considerations and recent empirical results suggesting that humans also have access to path integration mechanisms other than configural updating. Paths are usually curved structures not easily divisible into a low number of straight line segments as required by configural mechanisms such as the EEM. In addition, response times to point homeward at the end of a path have been shown to decrease with increasing path complexity if overall path length and turning angle are controlled for (Wiener and Mallot 2006). This result cannot be explained by configural path integration mechanisms. Furthermore, a recent fMRI study has shown that path integration in humans recruits a cortical system similar to that of rodents and non-human primates (Wolbers et al. 2007) for which path integration has been described as a continuous process. And finally, studies investigating spatial updating—the ability to update positions of external object locations while moving through space—suggest that humans can employ different modes of updating locations (Amorim et al. 1997). Spatial updating and path integration appear to be similar processes as both require the updating of positions in space based on ego-motion information. During spatial updating, however, these positions are external object locations while they are positions occupied by the traveler during path integration. FMRI studies on path integration (Wolbers et al. 2007) and spatial updating (Wolbers et al. 2008) suggest that different cortical systems are involved in representing and updating external object locations and locations occupied during navigation, indicating that spatial updating and path integration may also be dissociable on a functional level. Ongoing work in our laboratories appears to support this conclusion.

To the authors' knowledge, no study so far investigated continuous strategies in human path integration, which requires updating self-location (as opposed to external object locations, cf. Amorim et al. 1997). While it is conceivable that humans have access to continuous path integration mechanisms, experimental validation is required. This study was designed to systematically test and compare configural and continuous updating mechanisms in human path integration. Blindfolded participants were asked to solve triangle completion tasks after being carefully instructed to use either a continuous or a configural updating strategy (cf. Amorim et al. 1997). Path integration performance was assessed by accuracy measures (homing-, direction-, and distance-error) and response times. As path integration is sensible to error accumulation, we expected a general decrease in homing accuracy with increasing path length and turning angle. With respect to the two path integration strategies, we specifically expected faster response times in the continuous condition than in the configural condition; as outlined earlier, continuous path integration is an online process (the home vector is available at all times) whereas configural path integration is an offline process (the home vector is computed at the end of the outbound path). In addition to the performance-related

measures, we also monitored participants' head movements during navigation along the two outbound legs of the triangle. Earlier research on head movements suggests an important role of head orientation for the control of locomotion. Grasso et al. (1998), for example, reported anticipatory head movements on curved paths toward future walking directions (see also, Prévost et al. 2002; Hicheur et al. 2005; Sreenivasa et al. 2008). Such anticipatory head movements have been recorded even if participants were blindfolded (Courtine and Schieppati 2003). In this work, we explore whether head orientation can also serve as a motor expression of the home vector or the updating mode, respectively. If that was the case, we expect differences in head orientation during the outbound paths depending on the updating strategy.

Evidence in favor of multiple path integration strategies can also shed light on a number of inconsistent neuroscience findings. In support of animal findings, a number of lesion and fMRI studies have established an involvement of the medial temporal lobe in human path integration (Worsley et al. 2001; Philbeck et al. 2004). In contrast, Shrager et al. (2008) did not observe path integration deficits in patients with bilateral medial temporal lesions. This contradiction could be resolved if humans in fact had access to multiple path integration strategies that relied on different neuronal circuits.

Materials and methods

Participants

Sixteen healthy volunteers participated in this study. One participant was removed from the final data set, as homing errors exceeded the mean errors of the group by more than 2 standard deviations. All remaining 15 participants understood the instructions without difficulties and were naive with respect to the hypotheses at the time of testing (age range 19–35 years, 7 females).

The triangle completion tasks

A set of 16 paths that consisted of two segments each were composed. The paths differed in length of the first segment (4 m or 9 m), turning direction (left vs. right), turning angle (45°, 90°, 135°, 155°, 163°), and length of the second segment. As apparent from the middle panel in Fig. 1, the paths were designed such that each of the eight final positions was approached on two different outbound paths. While these path alternatives required the same home vector, one path was shorter and had a smaller turning angle than the other path. For the analysis, we therefore divided the 16 paths into 2 groups: (1) *short paths* with an

average length of 8.3 m and an average turning angle of 101° and (2) *long paths* with an average length of 15.3 m and an average turning angle of 148°.

Procedure

The experiment was carried out in the Tracking Laboratory (12 m × 15 m) of the Max Planck Institute for Biological Cybernetics in Tübingen (Germany). Participants were blindfolded and wore earplugs to eliminate both visual and auditory cues. They were equipped with 5 reflective markers fixed on a helmet. The 3D positions of the markers were recorded with a sampling rate of 60 Hz using an optical tracking system consisting of 16 cameras (Vicon).

To guide participants along the predefined paths, the experimenter gently pulled them using a wooden stick that participants held with both hands. Upon arriving at the endpoint of the outbound paths, the experimenter pushed down and released the wooden stick, signaling participants to start homing. They were instructed to turn on the spot until facing the direction of the origin before starting to home. Participants verbally informed the experimenter after arriving at the assumed home position. They were instructed to solve the homing tasks as fast and as accurate as possible. In order to eliminate any feedback about homing performance, participants were led back to the start place along long winding trajectories.

The experiment consisted of a training phase and a test phase

Training phase

To familiarize participants with the task and to minimize learning and habituation effects during the later test phase, we first performed extensive training. Each participant was led along all 16 outbound paths and was asked to home back to the start place. Participants did not receive any instructions about specific updating strategies in the training phase and were not given feedback regarding their path integration performance.

Test phase

The test phase was composed of two experimental blocks. In each block, participants were led along the 16 outbound paths and were asked to home back to the start place. In one block, participants were instructed to closely attend to the outbound path and to remember it. They were instructed to imagine the shape of the outbound path for retrieving (calculating) the home vector at the end of the outbound path (*configural condition*). In the other block, participants were instructed to continuously keep track of the starting location such that they would be able to
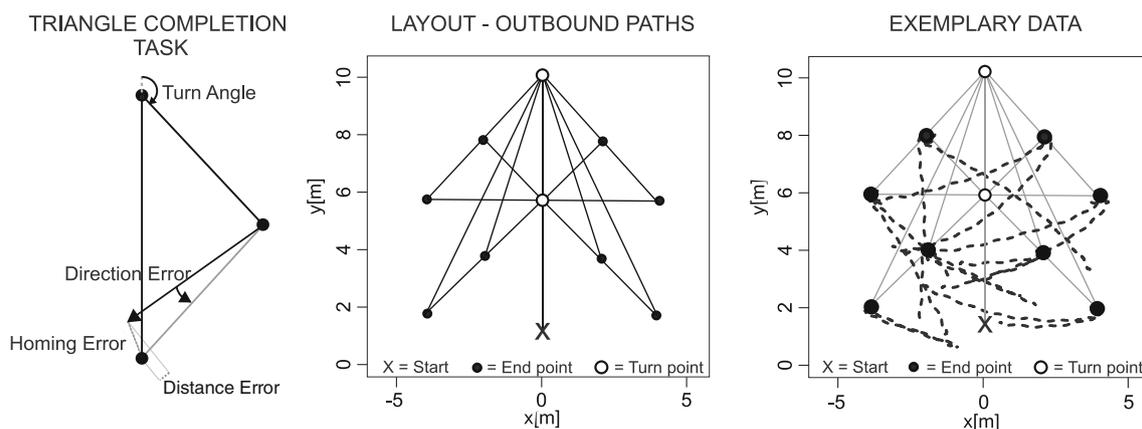
Fig. 1 *Left* The triangle completion task and homing accuracy measures; *middle* The layout of the 16 outbound paths; *right* Exemplary data of one participant in the configural condition (*dashed lines* represent homing trajectories)

instantly point to it at all times during navigation (*continuous condition*). The order of the configural and continuous condition was counter-balanced between participants, and the 16 paths were presented in a randomized order for each participant.

Analysis

Path integration performance was assessed by calculating homing error—i.e. the distance between the start point of the outbound path and the endpoint of the homing trajectory. In principle, homing error can result either from distance or direction errors alone or from a combination of distance and direction errors. We therefore also calculated distance and direction errors (see Fig. 1). In addition, response time was calculated for each trial; it was defined as the time between releasing participants at the end of the outbound path, until they crossed a virtual circle with a radius of 40 cm surrounding the end point of the path. Response times therefore include the time required to compute the home vector, to orient toward the start location, and to cover a distance of ∼40 cm after initiating homing. Finally, in order to assess the influence of the path integration strategy on locomotor behavior, we analyzed position and orientation of the participants' head—i.e. the position of the helmet that was tracked by the optical motion capture system—along the outbound paths. This allowed comparing participants' head orientation during locomotion between the configural and the continuous updating mode.

Results

Overall, 38 trials (5.3%) were removed from the final data set, as recordings from the tracking system were incomplete and trajectories could not be reliably reconstructed.

Homing error did not differ between left turn trials and right turn trials ($t(14) = -1.04$, $P = .31$). The order in which the test conditions were presented had no influence on participants' homing performance ($F(1, 14.3) = .23$, $P = .64$). For the further analyses, left and right turn trials were therefore pooled and order information was discarded. Figure 2 displays homing performance for two of the paths with identical final positions (i.e. release points).

Homing error

Neither for the configural condition nor for the continuous condition did we observe an improvement of path integration performance over the 16 trials (Pearson's product moment correlation: configural condition: $r = .04$, $P = .62$; continuous condition: $r = .04$, $P = .60$), showing that our training procedure successfully prevented any learning effects during the test phase. Collapsed across both path lengths, mean homing error was 2.18 m for the
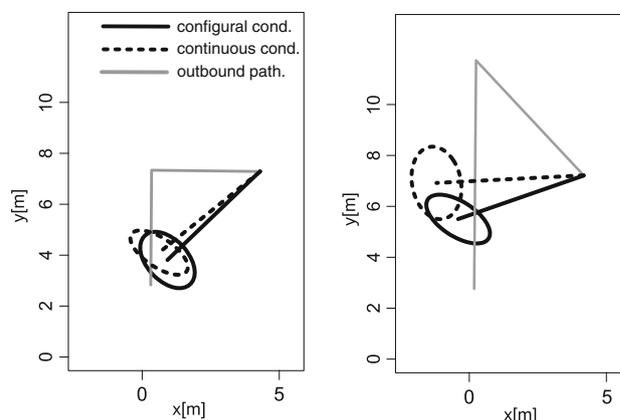

Fig. 2 Homing performance (95% confidence ellipse) for two of the paths with identical final positions

configural and 2.72 m for the continuous condition (Fig. 3). A 2 × 2 repeated measures ANOVA with factors path length (short vs. long) and condition (configural vs. continuous) revealed significant main effects of path length ($F(1, 14) = 20.12$, $P = .001$, partial-eta$^2 = .59$) and condition ($F(1, 14) = 11.37$, $P < .01$, partial-eta$^2 = .45$) as well as a significant interaction ($F(1, 14) = 6.64$, $P = .02$, partial-eta$^2 = .32$). Specifically, homing errors were smaller for the configural condition than for the continuous condition and for short paths than for long paths. Significant differences between the configural and the continuous condition were observed for long paths (t test: $t(1, 14) = 2.19$, $P < .05$, two-tailed) but not for short paths (t test: $t(1, 14) = .68$, $P = .51$, two-tailed), demonstrating that the two strategies only produced dissociable homing performance when tested with the long paths.

Absolute direction error

The overall pattern of the direction error was similar to that of homing error (Fig. 3). Mean absolute direction error was 21.90° for the configural and 25.40° for the continuous condition. A 2 × 2 repeated measures ANOVA with factors of path length (short vs. long) and condition (configural vs. continuous) revealed significant main effects of path length ($F(1,14) = 20.03$, $P = .001$, partial-eta$^2 = .59$) and condition ($F(1, 14) = 4.83$, $P = .045$, partial-eta$^2 = .26$). Specifically, direction error for the configural condition was smaller than for the continuous condition. While the interaction between path length and condition did not reach statistical significance ($F(1, 14) = 3.46$, $P = .08$, partial-eta$^2 = .20$), differences between conditions were more pronounced for long paths than for short paths. This

Fig. 3 Behavioral results (mean ± sem); *Top left panel* homing error; *top right panel* response times; *lower left panel* direction error; *lower right panel* absolute distance error
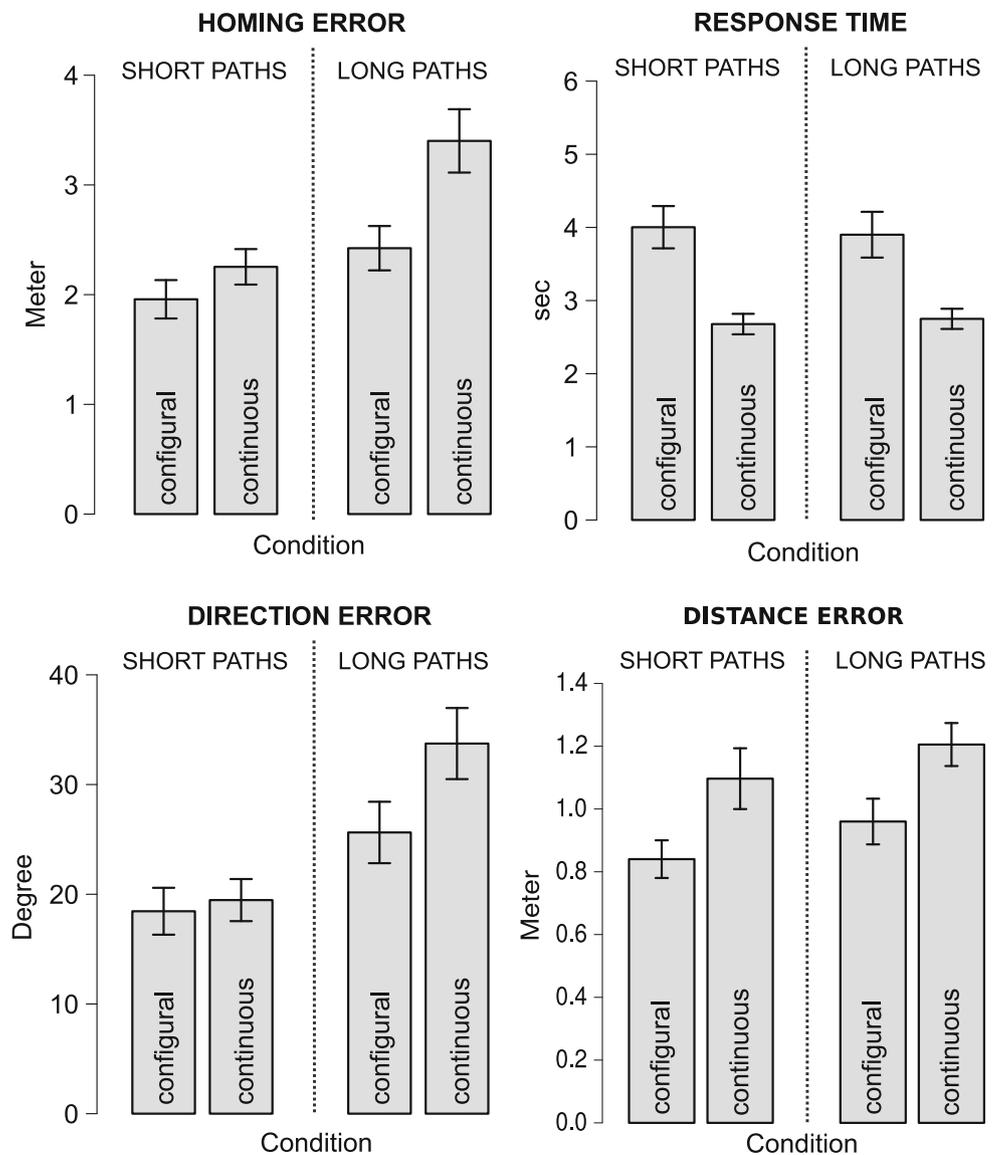
is corroborated by post hoc t tests revealing a significant difference between conditions for long paths ($t(1, 14) = 2.19$, $P < .05$, two-tailed) but not for short paths ($t(1,14) = -.68$, $P = .51$, two-tailed).

Absolute distance error

Mean absolute distance error was 0.90 m for the configural and 1.16 m for the continuous condition (Fig. 3). A 2 × 2 repeated measures ANOVA with factors of path length (short vs. long) and condition (configural vs. continuous) revealed a significant main effect of condition ($F(1, 14) = 7.02$, $P = .02$, partial-eta$^2 = .34$), a marginally significant effect of path length ($F(1, 14) = 3.6$, $P = .07$, partial-eta$^2 = .22$), and no significant interaction ($P = .93$). Specifically, distance errors were smaller in the configural condition when compared to the continuous condition.

Response time

Whereas homing-, direction-, and distance-errors were smaller in the configural condition, we observed opposite results for our response time measure (Fig. 3). A 2 × 2 repeated measures ANOVA with factors of path length (short vs long) and condition (configural vs. continuous) revealed a significant main effect of condition ($F(1, 14) = 16.05$, $P = .001$, partial-eta$^2 = .53$), while no effect of path type ($F(1, 14) = .03$, $P = .86$, partial-eta$^2 = .002$) and no interaction was found ($F(1, 14) = 2.35$, $P = .15$, partial-eta$^2 = .14$). The main effect for condition was driven by significantly shorter response times in the continuous condition than in the configural condition (2.70 vs. 3.95 s), strongly suggesting that participants engaged in homing vector computations at the end of the outbound path in the configural condition only.

Head orientation

The left panels of Fig. 4 display one participant's trajectories and head orientation data for the same outbound path in both experimental conditions. On the first leg, head orientation was closely aligned with the direction of travel and did not differ between both conditions. In contrast, on the second leg, the participant's head was deviated in direction of the origin. These results were confirmed on the group level (Fig. 4, right panels), with both conditions showing significant deviations from straight ahead (configural condition [2.88° vs. 0.0°]: t test: $t(14) = 5.10$, $P < .001$; continuous condition [7.43° vs. 0.0°]: t test: $t(14) = 7.38$, $P < .001$). Importantly, we also observed a significant difference between conditions on the second leg: in the continuous condition, participants' heads were more strongly deviated from straight ahead into the

direction of the origin (7.43°) than in the configural condition (2.88°; t test: $t(14) = 3.67$; $P = .002$, two-tailed).

In order to further analyze this effect, we calculated the slope of the deviation of head orientation from straight ahead over the traveled distance along the second segment. When compared to the overall bias reported earlier, this measure is sensitive to changes of head orientation during locomotion. The analysis of the slope revealed significant differences between conditions. Specifically, the mean slope in the configural condition was close to 0 ($<.01$) while it was significantly larger in the continuous condition (1.13; Wilcoxon's t test: $W = 46$; $P < .01$[1]) as well as different from 0.0 (Wilcoxon's t test against 0.0: $V = 108$; $P < .01$). These results demonstrate that participants increasingly turned their head in direction of the start place while locomoting along the second segment of the path in the continuous condition only.

Discussion

In this study, we investigated the effects of two distinct updating modes on human path integration. The continuous mode sought to resemble path integration processes as described in the animal literature in which ego-motion perception is used to update the distance and direction to the start place of the journey continuously (for an overview of path integration models in the animal literature, see: Benhamou and Séguinot 1995). The configural updating mode reflects path integration models proposed for humans when solving triangle completion tasks (Fujita et al. 1993). This mode requires encoding the outbound path, generating a survey representation of the path and computing a home vector when required—i.e. at the end of the outbound path.

Path integration performance

Results revealed systematic differences between the two path integration strategies, suggesting that task instructions in fact influenced participants' path integration modes. First, response times were shorter in the continuous condition than in the configural condition. This was expected as during continuous updating a home vector is computed online—i.e. during locomotion—and thus available at all times. In configural updating, on the other hand, the home vector is computed only at the end of the outbound path, resulting in increased response times (cf. Fujita et al. 1993). Second, path integration was more accurate (smaller

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[1] The right panel of Fig. 4 demonstrates substantial changes in head orientation at the beginning and the end of the second segment. As these head movements are likely to be related to whole body turnings, the first as well as the last 20 cm of the recordings of the head orientation along the second segment were discarded for this analysis.

Fig. 4 *Left column* Exemplary trajectories (*solid line*) including head orientation (*dashed lines*) along the same outbound path in both experimental conditions for one participant. Differences in head orientation between the continuous and the configural condition are apparent on the second segment; *Right column* Mean (*dashed line*) and standard deviation (*solid lines*) of head deviation across subjects and trials plotted against normalized covered distance along the second segment of the outbound paths. Positive values correspond to deviations in direction of the start position. The *horizontal line* corresponds to the expected head deviation if participants aligned their head with their direction of motion

HEAD ORIENTATION - CONFIGURAL CONDITION

HEAD ORIENTATION - CONTINUOUS CONDITION
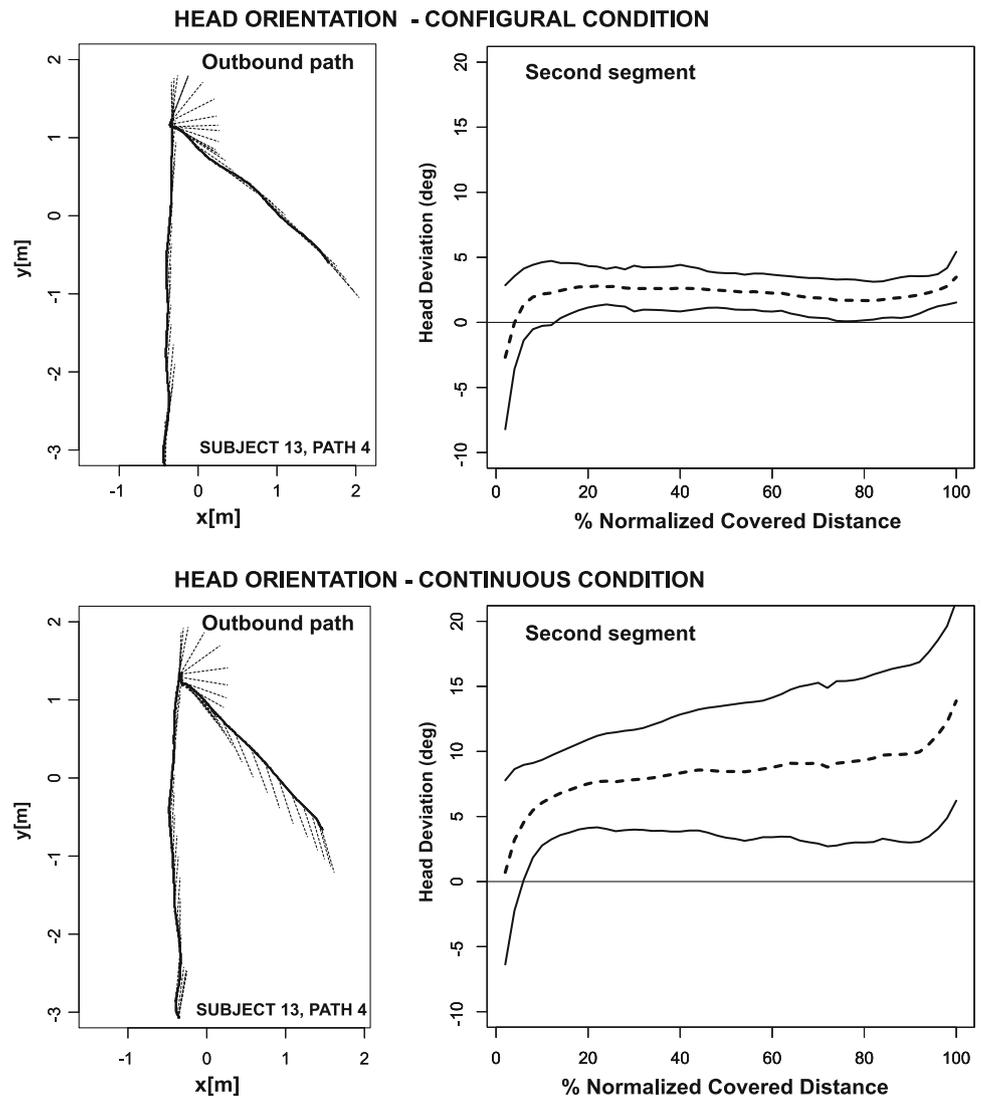
homing-, direction-, and distance-error) when participants were instructed to use the configural strategy when compared to the continuous strategy. There was, however, an interaction between path integration strategy and path length: while no differences were observed in homing error between configural and continuous path integration on short paths, participants performed more accurately when using a configural path integration strategy on long paths (direction error results show a very similar picture). This interaction can be explained by the use of the different path integration strategies: In continuous updating errors accumulate with traveled distance, an increase in homing error on long when compared to short paths was therefore expected. In configural updating, on the other hand, participants estimated the length of the individual segments. Many participants reported that they counted the number of steps for doing so. Assuming that single steps are similar in length, this method is less vulnerable to error accumulation. The accuracy of distance estimations is therefore widely independent of the length of the single segments. Moreover, this method provides path integrators with a good estimation of the relation of the lengths of the two outbound segments, which is crucial for calculating a precise home vector. This would also explain why similar homing error performance was observed on short and on long paths during configural updating. Even if participants estimated traveled distance by integrating perceived ego-motion from proprioception—which is more vulnerable to error accumulation than counting steps—dividing the outbound path into two discrete segments would always result in a reduction of overall error accumulation when compared to purely continuous updating.

Head orientation

Head orientation during walking was influenced by the path integration mode. Specifically, participants' head deviated from straight ahead in the direction of the origin

on the second leg of the outbound paths. While this effect was small (~ 2–$3°$) in the configural condition, deviation from straight ahead in the continuous condition was significantly larger ($\sim 7.5°$). Head movements during locomotion have been investigated in a number of studies. Head stabilization, for example, has been described for different locomotion tasks (Pozzo et al. 1990), suggesting that the control of locomotion relies on a head-based reference frame. Further studies demonstrated anticipatory head movements on curved paths with respect to the future walking direction (Grasso et al. 1998; Prévost et al. 2002; Hicheur et al. 2005). These anticipatory head movements remained even if participants are blindfolded (Courtine and Schieppati 2003).

In contrast to earlier studies investigating head movements during locomotion, we here demonstrate systematic deviations from straight ahead during blindfolded guided walking along linear paths. These deviations were apparent in both conditions along the second leg and increased in the continuous condition (see Fig. 4). It therefore appears unlikely that head movements were involved in the control of locomotion anticipating the immediate future walking direction. Rather, they reflect the spatial task (i.e., the integration of ego-motion). This is further corroborated by the difference of the deviations from straight ahead in the two conditions, strongly suggesting a top down influence of the cognitive updating mechanism on motor behavior—i.e. on head movements during locomotion. Specifically, head orientation appears to be a coarse indicator of the direction toward the starting location, thus forming a continuous motor expression of the home vector. When instructed to continuously keep track of the start position, participants constantly update the home vector online—i.e. during locomotion along the outbound path. As a consequence, the head is increasingly deflected in direction of the start place on the second leg of the outbound path. Conversely, when using configural updating strategies, participants predominantly attend to the traveled path rather than calculating the location of the start position during travel. The motor expression of this offline strategy is a lesser deflection of the head from straight ahead during the outbound path with no apparent changes in deflection along the second leg.

To the best of our knowledge, our study is the first to measure head orientation during locomotion but outside the context of locomotor control. Rather, we have demonstrated that head orientation can also reflect a cognitive process, in our case the cognitive strategy underlying path integration. Importantly, head orientation is qualitatively different from standard path integration measures such as response times or homing-, direction-, and distance-errors (e.g., Loomis et al. 1993): whereas these measures are offline indicators, head orientation constitutes an online measure that can inform about the updating mechanism already during locomotion.

The two-systems view of human path integration

Path integration performance measures, response times, and the head orientation data all suggest a reliable influence of the path integration strategy on behavior, both during the outbound path (head orientation) and during the return phase (homing accuracy and response time). Moreover, the response time data showed the expected pattern: faster response times for continuous updating—during which a home vector should be available at all times—than for configural updating—during which a home vector is computed only when required. Taken together, the results are consistent with the assumption that human path integration can be achieved using different cognitive mechanisms: Specifically, *continuous path integration* constitutes an online process during which perceived ego-motion is instantaneously used to update the home vector—an egocentric representation of the distance and direction to the start location. Purely continuous path integration thus does not require memorizing the configuration of the path traversed and the home vector is available at all times. During *configural path integration*, on the other hand, ego-motion information is integrated to form a representation of the path configuration. The home vector is computed on basis of this representation only if required. Configural path integration therefore constitutes and offline process. Continuous and configural path integration differ both in the timing of the home vector calculation and in the working memory demands.

While most earlier studies on human path integration discussed configural strategies (e.g., Fujita et al. 1993; Loomis et al. 1993; Klatzky et al. 1999), we predicted the existence of an alternative, continuous path integration mechanisms for different reasons. First, trajectories are not always easily divisible into a low number of straight line segments. Rather, paths are curved structures, which are often more complex than the outbound paths used in triangle completion experiments. Configural updating strategies such as described in the encoding error model (EEM: Fujita et al. 1993), however, cannot be applied to curved outbound paths. Second, recent work demonstrated that response times to point homeward at the end of a path decrease with increasing path complexity if overall path length and turning angle is controlled for (Wiener and Mallot 2006). This result cannot be explained with configural mechanisms in which the construction of a survey representation of a complex path consisting of more elements should take more not less time. Wiener and Mallot (2006) suggested a strategy shift from configural path integration mechanisms on simple paths to more

continuous mechanisms on more complex paths. Third, Wolbers et al. (2007) have shown that path integration in humans recruits a cortical system similar to that of rodents and non-human primates for which path integration has been described as a continuous process. Specifically, path integration seems to rely on the extraction of self-motion information in the human motion complex hMT+, spatial working memory processes in medial prefrontal cortex, and higher level spatial processes in the hippocampus. Finally, studies investigating spatial updating—the ability to update external object locations while moving through space— suggest that humans can employ both configural and continuous updating modes (Amorim et al. 1997). Taken together, these results suggest the existence of at least two path integration strategies—i.e. continuous and configural updating.

It is likely that different individuals utilize different strategies, depending on their preferences, on the exact nature of the paradigm, and on the layout of the outbound paths. For future path integration studies, it is therefore essential to identify the chosen strategy on an individual basis. With head orientation during locomotion, we have introduced a novel online measure for path integration that can inform about individual strategies.

Neural mechanisms underlying path integration

As our results demonstrate dissociable cognitive operations for human path integration, it is important to ask whether they involve dissociable (sub-)cortical mechanisms. In rodents, computations of position by entorhinal grid and hippocampal place cells and computations of orientation by head direction cells can provide the animal with online information about its current position and orientation relative to a starting location (Etienne and Jeffery 2004). As a consequence, damage to the medial temporal lobe should impair path integration performance, which has been confirmed in lesion experiments (Whishaw and Maaswinkel 1998; Maaswinkel et al. 1999, but see Alyan and McNaughton 1999). While these findings strongly suggest that the continuous path integration strategy thought to underlie animal homing behavior requires an intact limbic system, homing behavior is also impaired following lesions to the posterior parietal cortex (PPC, Parron and Save 2004). Given the established role of posterior parietal areas for egocentric spatial processing and the dense connections with medial temporal structures, the PPC is currently thought to use output from medial temporal lobe structures to compute the spatial relationship between the current location of the animal and a desired goal location (Byrne et al. 2007; Whitlock et al. 2008; Calton and Taube 2009). Hence, the primary deficit of rats with parietal lesions appears to be a difficulty in using medial temporal signals to compute homeward trajectories.

In humans, the importance of medial temporal structures for path integration has been established by neuroimaging and lesion studies (Worsley et al. 2001; Philbeck et al. 2004; Wolbers et al. 2007), but the precise contribution of posterior parietal areas is less clear. The PPC receives multiple types of self-motion information, including information about body movements from motor efference copies and somatosensory feedback, vestibular self-motion cues from the parieto-insular vestibular cortex and multi-modal self-motion cues from hMT+.

Importantly, given that areas such as hMT+ also have a working memory capacity (Pasternak and Greenlee 2005), it is conceivable that some integration of self-motion cues over time already occurs in early sensory areas. This information can in turn be used by posterior parietal structures to build up representations of the traveled segments of a path, which is consistent with recent findings showing that TMS applied over posterior parietal areas and chronic parietal lesions disrupt the ability to assess spatial displacements (Farrell and Robertson 2000; Seemungal et al. 2008). In other words, the configural updating strategy requires idiothetic self-motion sensing, but it does not involve continuous updating of position and orientation during the outbound path. Rather, it is based on memory traces of translations and rotations that are ultimately used to compute the path layout and the relationship between the self and the goal location.

We therefore propose that the two modes of path integration we have established rely on dissociable neural systems: while the continuous updating of one's position and orientation depends on the grid, place and head direction systems, the configural mode of storing estimates of rotations and translations during the outward journey is primarily a posterior parietal function. In both cases, the final computations of the egocentric spatial relationships between the self and the goal location occurs in posterior parietal cortex, and dense parieto-frontal projections allow for this spatial information to be translated into appropriate motor programs to reach the goal location.

Our two-systems view of human path integration also helps to resolve recent controversies regarding the role of the medial temporal lobe. Contrary to previous findings (Worsley et al. 2001; Philbeck et al. 2004), Shrager and colleagues did not observe impairments in a homing task in patients with bilateral medial temporal lesions, which led them to conclude that the hippocampus and the entorhinal cortex are not required for path integration (Shrager et al. 2008). Although one may question the reliability of the latter findings due to the small sample size and the small number of longer paths tested, several methodological differences likely account for the discrepant findings. For

example, Philbeck and coworkers (Philbeck et al. 2004) measured path integration ability with a target-directed walking task, a task in which subjects cannot form a configural representation of a traveled path segment and hence have to rely on a continuous updating of the distance covered. In contrast, Shrager et al. (2008) asked their patients to perform triangle completion by pointing toward the starting location, and they explicitly encouraged them to actively maintain the paths in mind during each trial. While this was done to ensure that the tasks could be performed within the span of working memory, it most likely biased participants toward using a configural strategy. Specifically, by storing estimates of translation and rotation in posterior parietal circuits, these patients could reconstruct the path layout at the end of each trial and determine the homing response without requiring online information about their current position and orientation relative to the starting location. Hence, the ability to construct a survey representation of an outward journey by combining distance and direction estimates, an ability that may be unique to humans, can allow such patients to perform well within the range of healthy controls. Future studies aiming to characterize the precise contribution of medial temporal and posterior parietal structures to human path integration therefore need to precisely assess individual strategies, for example by monitoring head orientation as shown here.

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