

Article

Exploring Effects of Boundaries on Path Integration—An Approach to Link Spatial Navigation Performance to Brain Activity Concepts

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Abstract

Digital maps increasingly replace paper maps because they are accessible, regularly updated, and customizable. Yet they often weaken spatial orientation skills and create technological dependency. One possible solution is supporting navigation without extra cognitive effort by designing maps that address spatially responsive brain cells. These cells are thought to be involved in the construction of an internal spatial representation. As animal studies have shown that the perception of environmental boundaries contributes to the stabilization of firing behavior, we examined boundary effects on path integration (PI) in screen-based and virtual reality (VR) settings. This allowed us to test whether the effect is robust across formats with different immersion and self-motion feedback. Participants completed PI tasks in a virtual arena while viewing a briefly displayed elevated line, wall, or no artificial boundary. It was expected that perceived boundaries would stabilize the activity of spatially responsive cells, such as grid cells. This is likely to contribute to a reduction in PI errors. Results showed a supportive tendency for the line condition, whereas the wall condition produced the highest errors. This pattern was comparable across both media. The findings suggest that the effect of spatial boundary cues depends on their design and perceptual properties.

Keywords: spatial navigation; path integration; boundaries; spatial cells; virtual reality



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1. Introduction

Digital navigation systems have fundamentally changed the way people orient themselves and navigate through space. Mobile map applications and turn-by-turn navigation systems provide efficient and convenient guidance while influencing the cognitive effort required for route planning and wayfinding. However, this convenience also comes at a cost: users increasingly rely on external guidance systems instead of actively processing spatial information themselves. As a consequence, opportunities to develop and maintain spatial orientation skills are reduced, often resulting in fragmented or less accurate cognitive representations of geographic space [1–4]. This becomes particularly problematic when technical support is unavailable or fails, and users must rely on their own spatial abilities, to orient themselves and return to previously visited locations using path integration (PI). PI refers to this continuous updating of one's position and orientation based on self-motion cues such as visual flow, vestibular input, and proprioceptive information [5].

This mechanism allows individuals to estimate their current and other positions even in the absence of explicit landmarks [6].

Recent findings in neuroscience, in combination with modern cartography, offer a new perspective on these challenges. Spatial navigation is supported by specialized neural systems, including place cells, grid cells, and border cells, which together contribute to the formation of an internal cognitive representation of space [7–12]. In particular, environmental boundaries and cardinal spatial structures appear to play an important role in stabilizing and aligning these neural representations [10,13–15].

Findings from animal research, complemented by human studies, suggest that spatial orientation may potentially be supported not only through external navigational guidance, but also through visual structures compatible with internal neural mechanisms of navigation and spatial memory [16].

This idea forms the basis of a “neurocartographic” research perspective that aims to integrate neuroscientific concepts of spatial orientation into the design of cartographic and navigational interfaces. This approach seeks to identify perceptible spatial structures that could activate neural mechanisms underlying orientation and navigation, such as the regular firing of grid cells that reflect spatial geometry [8]. Previous work has already shown that cardinal directions, boundaries, and geometric spatial structures can influence navigational performance and spatial memory [16,17]. However, evidence on whether experimentally introduced boundaries can systematically support behavioral PI performance remains limited [16].

2. Research Background and State of the Art

2.1. Spatial Navigation and Cognitive Representations of Space

Spatial navigation depends on the ability to acquire, process, and store information about the surrounding environment. During navigation, humans continuously integrate spatial information into internal cognitive representations that allow them to estimate directions, distances, and locations relative to one another [10]. These spatial cognitive representations, often referred to as cognitive maps, are fundamental for orientation, route planning, and spatial decision-making [18,19].

Traditionally, research in cartography and spatial cognition has focused on the influence of external spatial structures on the formation of these cognitive maps [20–22]. In particular, landmarks and environmental boundaries are considered highly relevant for navigation and spatial memory [23–25]. Landmark-based navigation research has demonstrated that salient environmental objects support orientation and facilitate the acquisition of spatial knowledge [25–27]. Likewise, studies in empirical cartography showed that (artificial) geometric structures such as grids or hexagons can improve object location memory and spatial recall [28,29]. At the same time, digital navigation technologies seem to reduce the necessity for active spatial processing increasingly. Turn-by-turn guidance systems provide efficient support but often prevent users from building comprehensive spatial representations of the environment [1–3]. Consequently, users frequently develop fragmented or incomplete cognitive maps and show reduced spatial learning during navigation tasks [1–3]. These findings have intensified the search for new approaches that support navigation while simultaneously promoting spatial orientation abilities rather than replacing them.

One particularly relevant navigation process in this context is PI. However, without external correction, PI is inherently bound to accumulating navigational errors over time, especially in large-scale or poorly structured environments [13].

2.2. Spatially Tuned Cells and PI

Recent neuroscientific findings provide important insights into the neural basis of spatial orientation and PI [6,30]. Research in both animals and humans identified several classes of spatially tuned cells that contribute to the representation of space, including place cells, head direction cells, grid cells, and border cells [7–12,31,32].

Among these cell types, grid cells are considered particularly relevant for PI [30,33]. Grid cells exhibit a characteristic hexagonal firing pattern that tessellates the environment and is assumed to provide a metric framework for spatial orientation and distance estimation [8,11,12]. In humans, grid cells can only be studied indirectly using non-invasive functional magnetic resonance imaging (fMRI) [34,35], this measured activity is called grid-cell-like representations (GCLRs) [6,34,35]. Previous studies demonstrated that stronger GCLRs are associated with improved PI performance [6,35]. The potential of grid cells becomes even clearer in their stability across different spatial contexts, trials, starting positions, and even in complete darkness, where other spatially tuned cell types are forced to destabilize [8,10,36]. When the environment changes, these representations can undergo remapping, meaning that the spatial firing pattern is reorganized or shifted so that the internal map is realigned with the updated environmental input [37,38]. In some cases, this process is also described as re-anchoring, especially when firing fields adjust to a new but task-relevant reference point [39]. This adaptive flexibility makes grid cells a promising neural basis for PI tasks and also highlights that grid-cell activity can couple tightly to external spatial structures [13,30,40]. Importantly, environmental geometry and spatial reference structures strongly influence the alignment and stabilization of grid-cell firing patterns [10,13–15]. Hardcastle et al. [13], for example, showed that navigational errors accumulate with increasing distance from environmental boundaries, suggesting that boundaries contribute to the correction and stabilization of internal spatial representations. Likewise, studies on border cells demonstrated that these neurons respond specifically to environmental boundaries such as walls or edges and contribute to anchoring grid-cell activity patterns to the surrounding environment [12,13,41].

Further evidence indicates that cardinal axes and geometric environmental structures influence the preferred orientations of GCLRs in humans [14,15,30,37]. Several studies suggest that environmental cardinal axes act as external reference frames to which GCLRs align [40,42]. This alignment process may contribute to the stabilization of internal spatial representations and consequently support PI performance. Environmental boundaries therefore appear to provide stable external reference frames that support the organization and stabilization of internal spatial maps [16]. Together, these findings suggest a close interaction between environmental geometry and neural mechanisms of spatial navigation.

2.3. “Neurocartographic” Implications of Spatial Navigation Research

The growing understanding of spatially tuned cells opens new perspectives for cartographic and navigational research. Traditional approaches in navigation assistance mainly focus on optimizing external guidance through landmarks, symbols, or route instructions. ‘Classical’ landmark-based approaches face important limitations, as the salience and navigational relevance of landmarks strongly depend on individual experience, contextual interpretation, and task demands [43,44]. Consequently, identifying universally effective navigational cues remains challenging. In contrast, “neurocartographic” approaches aim to support the internal neural mechanisms underlying spatial orientation itself.

From this perspective, cartographic elements such as cardinal axes, boundaries, or geometric spatial structures may function not merely as visual aids, but also as stabilizing reference frames for neural spatial representations. Such structures could potentially support navigation and spatial memory without requiring additional cognitive effort from

users. Beyond boundaries, recent “neurocartographic” approaches also discuss whether geometric spatial structures aligned with the hexa-directional organization of grid-cell firing patterns may support spatial memory and navigation performance [16]. These visual structures are then thought to interact with neural mechanisms underlying spatial orientation and memory formation. This idea represents a conceptual shift in cartographic research, as it links map and interface design directly to neuroscientific mechanisms of orientation and memory.

Preliminary evidence already supports this assumption. Studies indicate that cardinal axes and environmental boundaries may have an impact on navigation performance as well as spatial orientation behavior [16,17]. Nevertheless, empirical research explicitly investigating artificial boundaries as “neurocartographic” elements that may support PI performance remains limited [16].

In particular, it is still unclear which types of artificial boundaries facilitate or interfere with navigation performance. While environmental boundaries are generally considered beneficial for stabilizing spatial representations, highly salient or obstructive barriers may also disrupt orientation processes by fragmenting the perceived environment or interfering with spatial perception [14,15]. Consequently, the influence of artificial boundaries likely depends on their visual salience, geometry, and temporal presentation.

Investigating these mechanisms experimentally requires environments that combine high experimental control with ecologically valid navigation behavior. VR provides a methodological framework that combines experimental control with more naturalistic navigation behavior. Immersive VR enables controlled manipulation of spatial features while additionally providing vestibular and proprioceptive cues relevant for path integration [45–51]. In contrast, screen-based paradigms—commonly used in fMRI—restrict self-motion signals and limit ecological validity. Thus, VR-based approaches offer a complementary bridge between highly controlled laboratory paradigms and realistic navigation behavior.

2.4. Research Gap and Hypothesis

Despite increasing evidence for interactions between environmental boundaries and spatially tuned neural systems, several open questions remain. First, it is still unclear whether briefly presented artificial boundaries can systematically improve behavioral PI performance in humans. Second, the extent to which such effects generalize across different levels of immersion and presentation formats remains largely unexplored.

Against this background, the present studies investigate whether boundaries can influence navigational performance in virtual environments. Participants completed PI tasks in either a monitor-based or an immersive VR setup while being exposed to one of three conditions: a briefly visible wall, raised ground-line, or no artificial boundary as control condition. Building on neuroscientific findings regarding the stabilizing role of environmental cardinal axes for spatial representations [13,14,30], we hypothesized that:

H1. *Environmental boundaries improve PI performance.*

Furthermore, because the proposed “neurocartographic” mechanisms are assumed to operate independently of specific display technologies, we expected that:

H2. *The effects of boundaries on PI performance generalize across different levels of immersion and presentation formats (monitor-based vs. immersive VR).*

3. Materials and Methods

Both studies received ethical approval from the Faculty of Geosciences Ethics Committee at Ruhr University Bochum and follow the principles of the Declaration of Helsinki [52]. Due to the varying duration of the experiments, subjects received a payment of 5.00€ for participating in the monitor-based study (approximately 30 min) and 7.00€ for the VR study (approximately 40 min).

3.1. Participants

The group of participants for both studies consisted mainly of individuals from the student community at Ruhr University Bochum. The requirements for participation included normal or corrected vision and no previous psychological or neurological conditions. After completing the recruitment of participants and prior to the statistical analysis of the collected data, individual or, if necessary, all trials of a participant were excluded based on experiment protocols and the analysis of visual representations of the traversed paths. This applied if technical difficulties, serious comprehension or control problems, or navigational strategies (e.g., re-tracing PI patterns, backward movements, etc.) contrary to the provided task instructions were detected (see also Section 3.5 Statistical Analysis).

These criteria led to the exclusion of 11 participants, resulting in a final sample of 43 participants (21 males, 21 females, 1 non-binary) in the monitor-based study for further statistical analysis. Their age ranged from 19 to 37 years with an average age of 25.88 years ($SD = 4.58$).

Nine subjects had to be excluded from the VR study due to the listed criteria, hence the analysis was conducted with a sample size of 43 participants (20 males, 23 females). The mean age was 25.95 years ($SD = 4.12$, range between 19 and 38 years). A minimum of 43 test subjects in each of the two experiments could therefore be either fully or partially included in the further statistical analysis. This is in line with the a priori sample sizes determined for a repeated-measures ANOVA using G*Power (version 3.1.9.7) ($f = 0.25$, $\alpha = 0.05$, $1 - \beta = 0.95$, 3 measurements, $r = 0.50$, $\varepsilon = 1$). Because the observed data were not normally distributed, the final inferential analysis was carried out using the Friedman test, followed by Wilcoxon post hoc tests.

3.2. Materials

An experimental 3D environment was developed using the Unity game engine (versions 2022.3.36f1 and 2022.3.58f1) and the Unity Experiment Toolbox (version 1.0) [53]. This toolbox was used to implement basic experiment design logic such as trial randomization, stimulus lists and experiment data recording. The created 3D environment consisted of a flat plane with a grass-like texture that either stretched to the horizon or was enclosed in a circular arena by a mountain range without any clear landmarks. Both skyboxes (default skybox without mountains and mountain skybox, see Figure 1) were rendered at infinity so that participants could not reach the edge of the experimental environment and visual flow resulted exclusively from the ground texture and rotation. The monitor-based study was conducted on a 2D computer screen, where participants navigated using a joystick (model: Logitech Extreme 3D Pro Joystick). This allowed them to move in all directions with a constant speed of 8 km/h (2.222 m/s) and rotate horizontally around their own axis by tilting or twisting the joystick in the desired direction (see Figure 2a). A HTC Vive Pro Head-Mounted Display (HMD) with wireless adapters for unrestricted rotation and corresponding controllers served as output and input devices for the second study conducted in a VR environment. The HMD was tracked via 4 Lighthouse tracking stations on tripods in the same quiet laboratory setting. Here, participants navigated using a combination of controller-assisted forward movement with a variable speed input of maximum 15 km/h

(4.167 m/s) (see Figure 2b) and physical rotation around their own body axis. A small circular carpet served as an anchor point in the physical space.

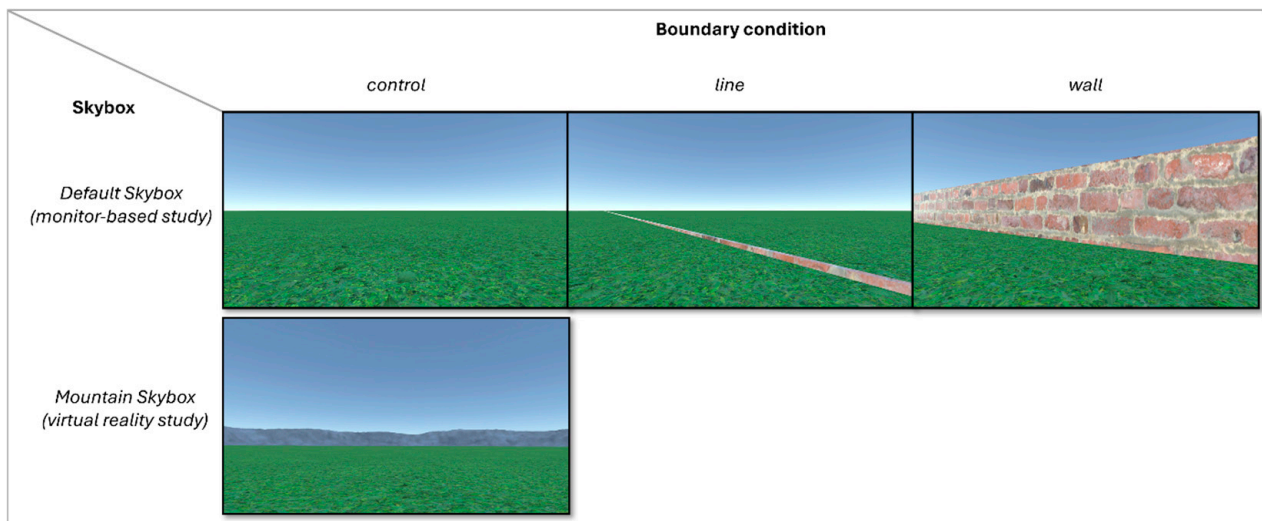


Figure 1. Two different skyboxes and similar boundary conditions were displayed in the experimental studies. To visually convey rotational movement not solely through the optical flow of the floor texture, an infinity-rendered skybox in the form of a gray mountain range without any distinctive reference points was additionally implemented in the VR follow-up study.

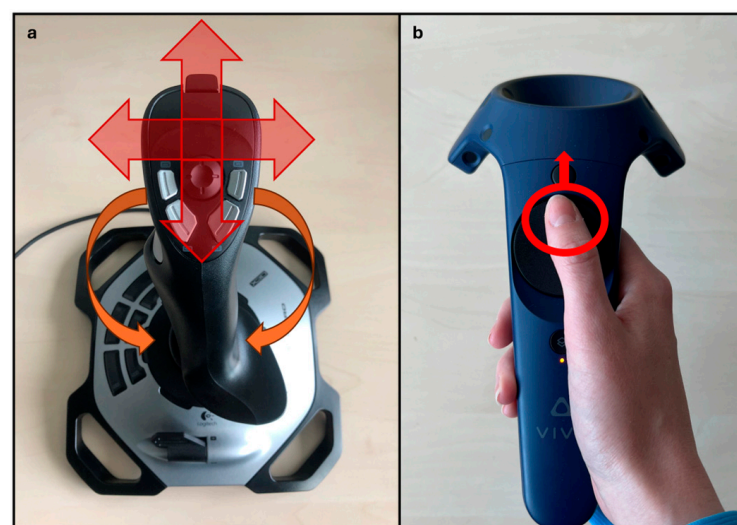


Figure 2. Input devices used for both experimental studies: A Logitech Extreme 3D Pro Joystick enabled constant movement in all directions (red arrows) and horizontal rotation in the monitor-based study design (orange arrows, (a)). The trackpad of a HTC Vive Pro controller allowed variable speed input during their forward movement in the VR study setup ((b), red arrow). To change direction, participants additionally had to rotate themselves in the desired direction, while standing on a circular carpet (not pictured).

3.3. Procedure

Before participating in a study, subjects signed an informed consent form and received written instructions. Each trial consisted of a PI task in which the participants had to navigate to three markers appearing one after the other in the arena before directly returning to the position of the first, now invisible, PI point without assistance and any detours (see Figure 3a). After logging their position, and depending on the magnitude of their distance error, they were awarded with up to three virtual coins, which were continuously collected as motivational feedback. At the start of a trial, movement was blocked for 5 s. Comparable

to a traffic light system, a color change of the start marker from red to green signaled that the movement restriction had been lifted. To prevent any confusion with the other identically shaped PI markers and to visually emphasize the special nature of the start marker position to be remembered, its shape was later changed from a cylinder to a cone for the VR study. Depending on the boundary condition, a space-structuring element in the form of a brick wall or a similarly textured raised line on the floor appeared at the beginning of the trial. While the latter was visible on the ground as an elevated structure measuring only 0.2 m in height and 0.2 m width, the brick wall was similarly wide but significantly higher with 4 m. In the control condition, neither the wall nor the line was visible. Upon contact with the first PI position (cylinder or cone), the space-structuring boundary disappeared (see Figure 4). This decision was intended to ensure equal exposure durations to the boundary cues across participants and to maximize the likelihood that the cues could influence internal spatial representations before the PI task began. We deliberately opted against a continuously visible boundary, because such a stimulus would have functioned as a permanent spatial reference and could have influenced navigation beyond the intended transient cue effect. The wall condition was deliberately implemented despite its potentially obstructive character because walls represent one of the most extensively studied environmental boundary types in spatial navigation and border-cell research [13,54,55]. Comparing the wall with a minimally intrusive raised ground-line therefore allowed us to investigate whether different visual and geometric boundary properties differentially affect PI performance. While developing the VR study, we decided to let the boundary elements fade in and out over the course of 3 s. This was to avoid an abrupt change in visibility that might otherwise have been perceived as a jump within the virtual environment.

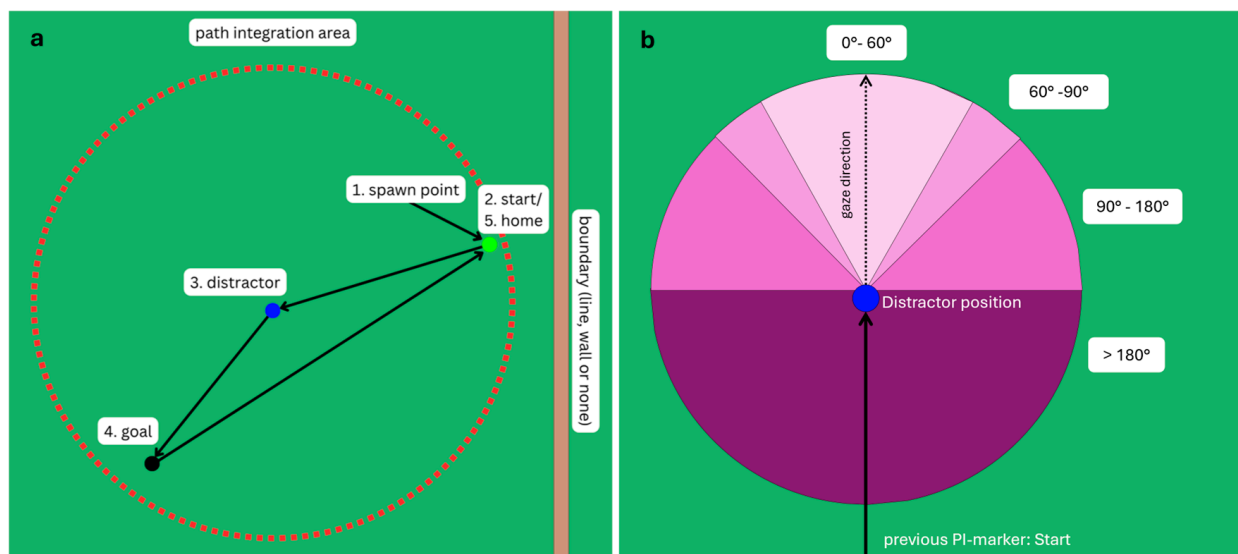


Figure 3. (a) Schematic top view of the arena layout and an example sequence for a PI task. Participants started from a spawn point and moved successively to PI positions 2 (start), 3 (distractor), and 4 (goal) before aiming to accurately locate the target position 5 (home). Depending on the boundary condition, a raised line (line), a similarly textured brick wall (wall), or no boundary (control) was visible at a fixed location outside the invisible PI area (red circle). (b) Based on the participants' gaze direction at the distractor marker, we distinguish between different angle conditions of 0–60°, 60–90°, 90–180°, and >180° for the next goal marker appearance. The perception of rotation is likely more challenging without additional visual reference points, or in the case of the monitor-based study, even without proprioceptive cues. Therefore, we consider the associated rotation degree as a difficulty factor for the PI task, which was balanced across condition blocks.

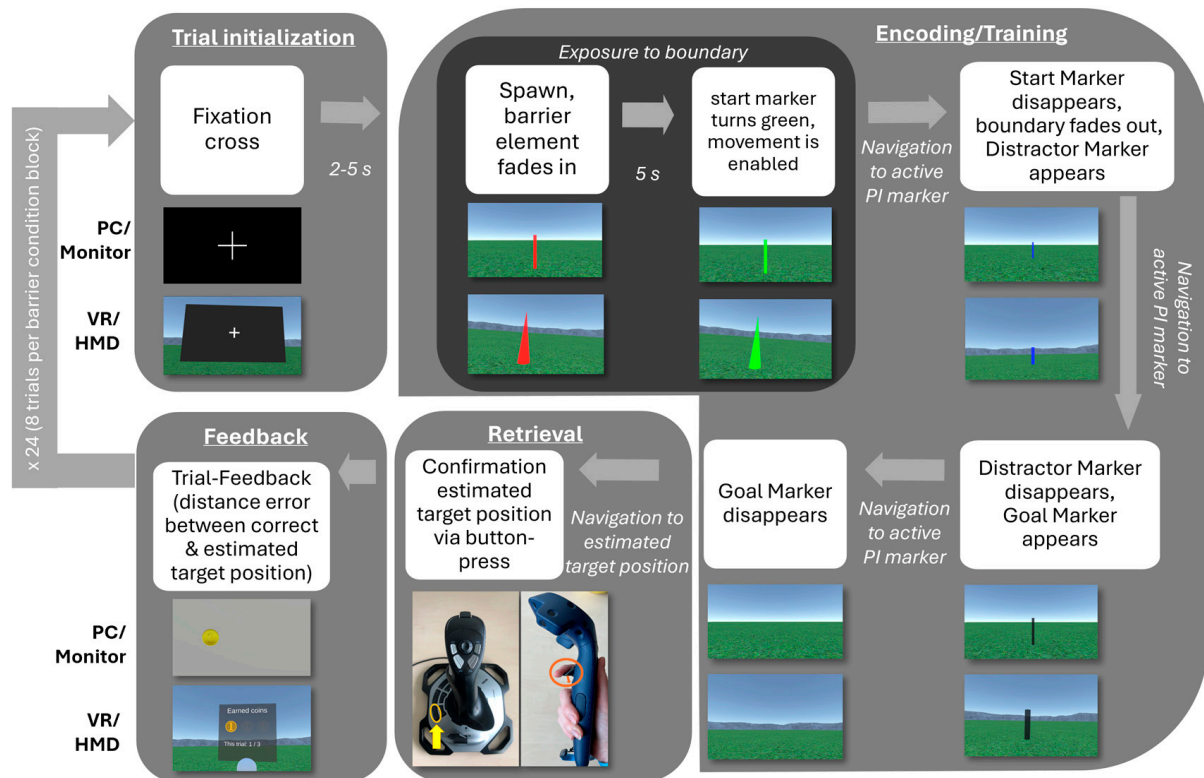


Figure 4. Schematic flow chart of a PI trial for both study designs, illustrated with first-person views of the virtual test environment across all task phases.

The PI position patterns were identical in both studies, ensuring that the data was comparable. The total distances of the PI patterns (starting from the spawn position to start/home, distractor, goal and back to start/home) varied between 40.52 m and 97.39 m ($M = 73.02$ m). For the random generation of PI patterns, we developed a PI Pattern Generator to meet our specific needs [56]. To ensure that all participants were equally exposed to the boundaries from the very beginning of each trial, the start marker was always placed within their field of view together with any visible boundaries, thereby allowing for a potential stabilization or alignment of grid cell patterns along these spatial structuring elements during the initial immobility phase. The patterns were grouped into three blocks, with the total PI distances and angle conditions distributed evenly. By angle condition, we are referring to various angle sizes ($0-60^\circ$, $60-90^\circ$, $90-180^\circ$, $>180^\circ$) at which the goal marker appears in the respective PI pattern when the distractor marker is reached, based on the participant's gaze direction (see Figure 3b). The rationale behind this categorization and balanced distribution across all condition blocks is the assumption that PI patterns in which no excessive rotation is necessary to view the goal PI marker may also be easier to complete. Particularly in the monitor-based study, where no proprioceptive but only visual cues are available regarding the extent of the rotation performed, excessive rotation likely leads to larger rotational errors. Another contributing factor in this regard is the absence of other visual reference points aside from the respective PI marker, which might otherwise serve as a guide to how much the participant has rotated. Both the condition assignment of the PI pattern blocks and the order of the trials within the blocks were randomized. This prevented certain boundary conditions from being paired with patterns that were too easy or too difficult, which could have biased participants' performance in favor of one condition over another. The order of the boundary conditions was assigned to each participant in a pseudorandomized order. Each of the three condition blocks consisted of 8 trials, resulting in a total of 24 trials in both experimental studies (see Figure 4).

3.4. Measures

To compare PI performance across all boundary conditions, distance and absolute angular deviations between the selected and correct target positions were used as performance measures. These metrics capture how accurately participants reproduced the previously learned target position for each PI pattern. In this case, we understand the task performance measure of the absolute angular error as the angular deviation between the estimated and correct target position relative to the last distractor position in degrees. The distance error is calculated as the Euclidean distance between the selected and correct target positions in meters (see Figure 5).

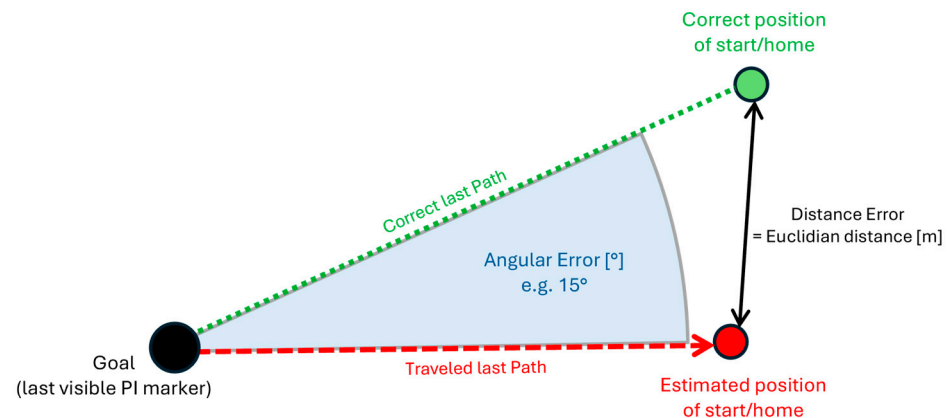


Figure 5. The variable angular error is calculated as the deviation between the estimated and correct target position of the start/home marker relative to the last visible PI marker position (goal) in degrees. The variable distance error is calculated as the Euclidean distance in meters between the estimated and correct position of the start/home marker.

3.5. Statistical Analysis

Prior to aggregating the collected data sets for statistical analysis, the data were pre-screened and cleaned. We defined the criteria for this to be the implementation of strategies in the PI task that did not correspond to the initially provided instructions. For this purpose, the participants' paths for all trials were visualized using an RStudio script (R version 4.4.1) [57]. This procedure was implemented as part of the data cleaning process to identify potential strategy use that violated the task instructions (using the shortest way back to the start/home marker), which might otherwise have remained undetected and artificially inflated performance. If violations, such as tracing back PI positions or (in the case of the monitor-based study) backward movement to avoid excessive rotation (see Figure 6), could be detected by visual evaluation, individual or, in the worst case, all trials of the participant were excluded from the data aggregation. The latter was done when fewer than 50% of trials were available, corresponding to less than four trials per condition for the subsequent calculation of mean values. In addition to the strategies mentioned above, technical problems, motion sickness, lack of concentration on the part of the participants, or similar incidents recorded during the tests were also considered during data cleaning. Participants whose mean distance errors exceeded more than two standard deviations from the overall mean (only values larger than the overall mean) were removed from analyses due to the risk of inattentiveness or disorientation. For the monitor-based study, this meant that 964 (93.41%) of the trials were suitable for statistical analysis, whereas in the VR-based study 963 trials (93.31%) could be included.

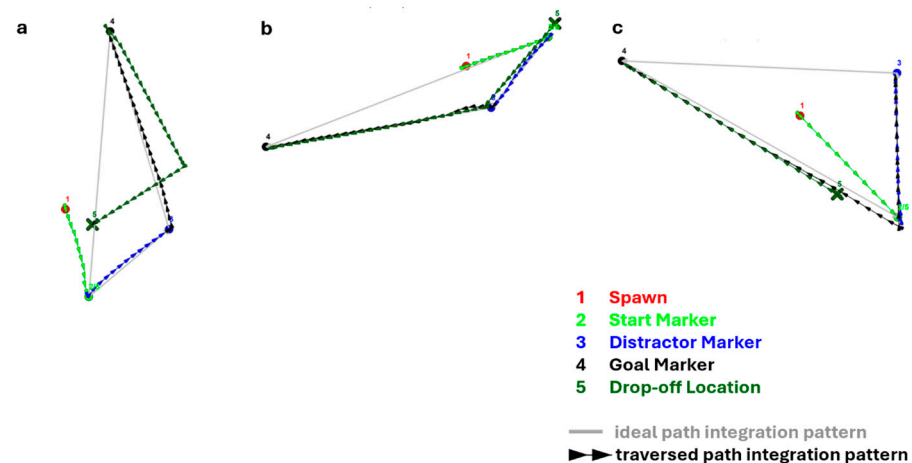


Figure 6. Exemplary traversed path visualizations from the monitor-based study in which the participants acted contrary to the task but still performed well due to their established strategies. (a) Participant retraced the last path along the PI markers; (b) participant retraced the last path along the PI markers but navigated backwards; (c) participant always returned to the correct position of the start marker on all paths while navigating backwards. These learnings led to a further development of the VR follow-up study, in which the direction of movement was restricted to only forward. In addition, an auditory signal (plop sound) now indicated when a marker position had been reached.

To decide which parametric or non-parametric test procedures to use, both experiments and their variables distance error in m and absolute angular error in $^{\circ}$ were subjected to graphical evaluation of histograms and analytical tests to determine normal distribution. Normality was assessed using visual inspection of histograms as well as formal tests, including the Shapiro–Wilk test. Across all combinations of variables (distance error, absolute angular error) and experimental conditions (control, line, wall), the results consistently indicated deviations from normality.

In addition to the evaluation of descriptive statistics for the variables distance error and absolute angular error per boundary condition, nonparametric Friedman tests were therefore performed to check for any significant differences between the boundary condition and these two performance measures. Additional post hoc tests (Wilcoxon signed rank test) with Bonferroni correction for pairwise comparisons were conducted, to reveal significant differences between the exact boundary condition pairs. These statistical tests aim to answer the first hypothesis, namely whether artificially implemented boundaries in both virtual experimental environments have a positive influence on PI performance. This could consequently be an indicator of a supportive function of the elements in stabilizing and aligning grid cell firing fields and border cell activities.

Further nonparametric Mann–Whitney U tests for independent samples were also conducted to examine the differences between the general PI performance averaged across all conditions for both distance error and absolute angular error in relation to the display format used (PC/monitor vs. VR/HMD). To better assess the extent of these differences, effect sizes (r) were calculated and interpreted according to thresholds developed by Cohen [58] ($r \approx 0.1$: small, $r \approx 0.3$, medium, $r \geq 0.5$: large).

The tests aimed to investigate whether the effects of artificial boundaries on PI performance generalize across both VR and monitor-based settings to support our second hypothesis (H_2) that spatial structures can influence navigation irrespective of the level of immersion.

4. Results

4.1. Monitor-Based Path Integration

The descriptive analysis showed that the PI performance of the participants, as represented by the variables distance error and absolute angular error, was best under the influence of the line as a virtual boundary element with the lowest mean error values ($M_{\text{lineDistanceError}} = 16.69$ m, $SD_{\text{lineDistanceError}} = 10.09$ m, $M_{\text{lineAbsoluteAngleError}} = 36.86^\circ$, $SD_{\text{lineAbsoluteAngleError}} = 31.22^\circ$), closely followed by the control condition ($M_{\text{controlDistanceError}} = 17.47$ m, $SD_{\text{controlDistanceError}} = 10.13$ m, $M_{\text{controlAbsoluteAngleError}} = 38.92^\circ$, $SD_{\text{controlAbsoluteAngleError}} = 34.70^\circ$). The highest mean distance and absolute angular errors were recorded in the trials in which the participants were exposed to the virtual wall ($M_{\text{wallDistanceError}} = 18.52$ m, $SD_{\text{wallDistanceError}} = 10.16$ m, $M_{\text{wallAbsoluteAngleError}} = 44.59^\circ$, $SD_{\text{wallAbsoluteAngleError}} = 37.36^\circ$) (see Figure 7a,c).

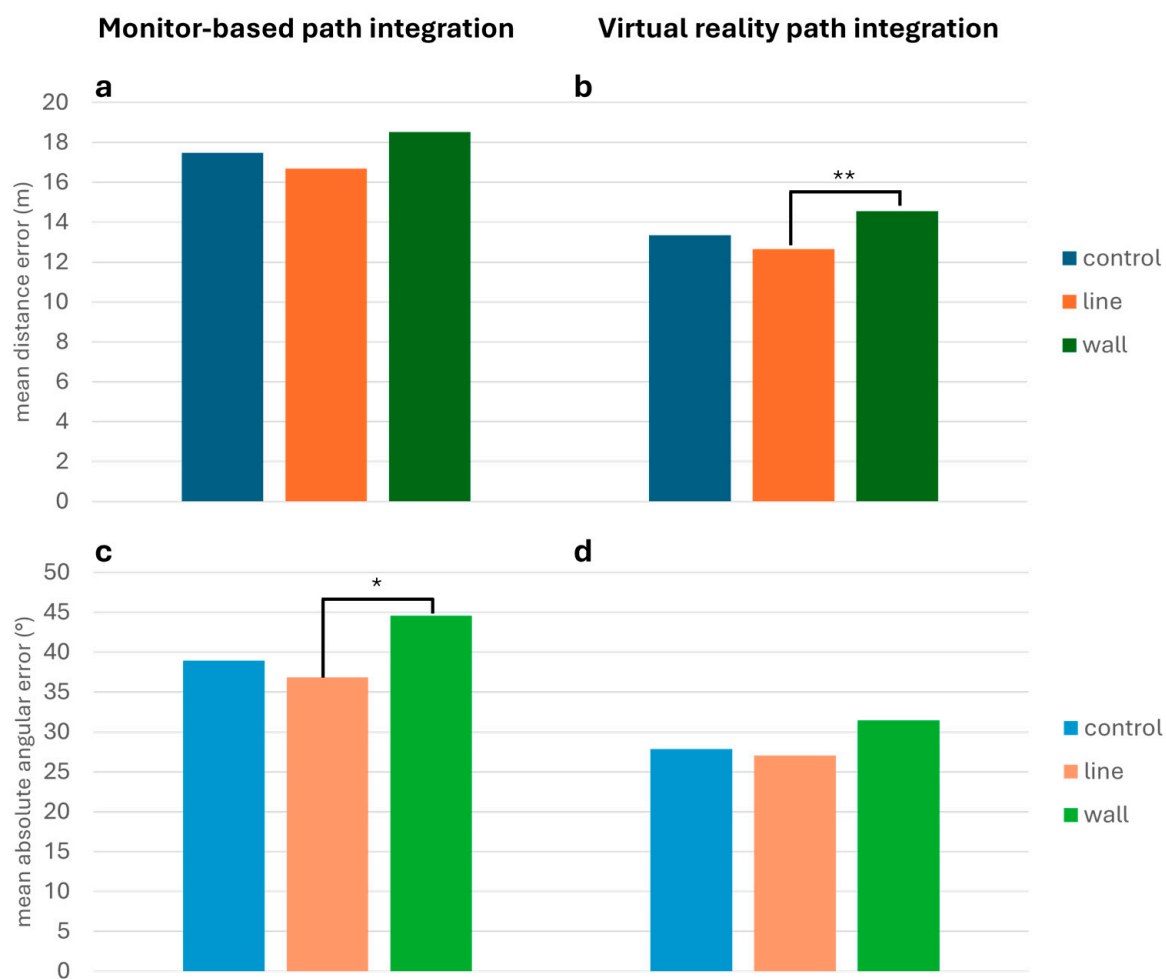


Figure 7. Descriptive mean values for the variables distance error (in m) and absolute angular error (in °) for each barrier condition control (blue), line (orange) and wall (green) in the monitor-based PI (a,c) and VR PI study (b,d). Statistical significance indicators correspond to: * $p < 0.05$, ** $p < 0.001$, *** $p < 0.001$.

A Friedman test on distance errors revealed no significant effect of the boundary condition, ($\chi^2(2) = 4.23$, $p = 0.121$). Non-parametric Wilcoxon tests for paired samples were thus conducted exploratorily. Post hoc p -values were Bonferroni-corrected. No significant differences emerged between control and line conditions ($W = 559$, $p_{\text{bonf}} = 0.906$) or between control and wall conditions ($W = 349$, $p_{\text{bonf}} = 0.408$). The line vs. wall comparison initially reached significance ($W = 288$, $p = 0.026$). However, this effect showed a trend after Bonferroni correction ($p_{\text{bonf}} = 0.078$).

For absolute angular errors, a Friedman test showed a statistically non-significant tendency for condition ($\chi^2(2) = 5.63, p = 0.060$). Non-parametric paired Wilcoxon tests were conducted exploratorily in this context. Post hoc p -values were Bonferroni-corrected. No significant differences appeared between control and line conditions ($W = 541, p_{\text{bonf}} > 0.999$) or between control and wall conditions ($W = 318, p_{\text{bonf}} = 0.186$). In contrast, a significant difference was found between line and wall conditions ($W = 251, p_{\text{bonf}} = 0.022$).

4.2. Virtual Reality Path Integration

Participants from the VR-study produced the lowest mean error values for both the distance error and absolute angular error during the line condition ($M_{\text{lineDistanceError}} = 12.65$ m, $SD_{\text{lineDistanceError}} = 7.5$ m, $M_{\text{lineAbsoluteAngleError}} = 27.02^\circ$, $SD_{\text{lineAbsoluteAngleError}} = 27.25^\circ$), closely followed by the control condition ($M_{\text{controlDistanceError}} = 13.34$ m, $SD_{\text{controlDistanceError}} = 7.98$ m, $M_{\text{controlAbsoluteAngleError}} = 27.84^\circ$, $SD_{\text{controlAbsoluteAngleError}} = 25.25^\circ$). The highest mean errors and thus the lowest PI performances were recorded in the wall condition ($M_{\text{wallDistanceError}} = 14.55$ m, $SD_{\text{wallDistanceError}} = 7.84$ m, $M_{\text{wallAbsoluteAngleError}} = 31.48^\circ$, $SD_{\text{wallAbsoluteAngleError}} = 27.2^\circ$) (see Figure 7b,d).

A Friedman test for distance errors indicated a significant effect of condition ($\chi^2(2) = 8.512, p = 0.014$). Confirmatory paired Wilcoxon signed-rank tests with Bonferroni correction were therefore conducted. No significant differences emerged between control and line conditions ($W = 562, p_{\text{bonf}} = 0.856$) or between control and wall conditions ($W = 336, p_{\text{bonf}} = 0.298$). However, distance errors differed significantly between line and wall conditions ($W = 226, p_{\text{bonf}} = 0.009$).

For absolute angular errors, a Friedman test yielded no significant effect of condition ($\chi^2(2) = 2, p = 0.368$). Exploratory paired Wilcoxon tests revealed no significant pairwise differences after Bonferroni correction: control vs. line ($W = 511, p_{\text{bonf}} > 0.999$), control vs. wall ($W = 324, p_{\text{bonf}} = 0.219$), and line vs. wall ($W = 349, p_{\text{bonf}} = 0.408$).

4.3. Comparing Path Integration Performance Between the Monitor-Based and Virtual Reality Study Design

A descriptive comparison as well as two nonparametric Mann–Whitney U tests for independent samples were performed to compare PI performance between the monitor-based and VR groups. The descriptive value ranking in which the respective conditions deviated in terms of both the distance error and the absolute angular error between the correct and selected PI position remained identical for both experiment designs (from lowest to highest PI error values: line—control—wall). However, participants in the monitor-based study produced higher average error values in all three conditions than participants in the similar VR environment (see a vs. b and c vs. d in Figure 7).

To identify differences between the cross-condition, monitor-based, and VR PI performance, two Mann–Whitney U tests were calculated for the two variables distance error and absolute angular error. For this purpose, the error values for each participant were averaged across conditions beforehand. Participants in the VR condition ($N = 43, M = 13.6$ m, $SD = 3.21$) showed significantly lower mean distance errors than participants in the monitor-based condition ($N = 43, M = 17.7$ m, $SD = 4.35$), $U = 458, z = -4.029, p < 0.001, r = 0.43$ (medium effect size [58]). Similarly, mean absolute angular errors were significantly lower in the VR condition ($N = 43, M = 29.0^\circ, SD = 7.88$) in comparison to the monitor-based condition ($N = 43, M = 40.5^\circ, SD = 12.6$), $U = 455, z = -4.055, p < 0.001, r = 0.44$ (medium effect size [58]).

5. Discussion

The present study investigated the influence of environmental reference structures such as local boundaries (cardinal axes) on human PI performance. It explored whether

the observed behavioral effects are consistent with current neuroscientific concepts of spatial navigation, particularly those related to grid cell mechanisms. The findings provide several important insights into the interaction between external spatial reference structures and internal spatial representations. While the observed behavioral effects are consistent with current neuroscientific models of spatial navigation, it is important to note that no direct neural measurements were obtained in the present study. Therefore, all references to grid-cell-related mechanisms remain theoretical and based on prior literature.

The first important finding was that participants consistently showed improved navigation performance when a cardinal axis was implemented as a raised line on the floor. Although these effects did not reach statistical significance, the repeated trend observed across modalities indicates a systematic influence of cardinal reference structures on navigation behavior. Importantly, this facilitation effect emerged not only in highly immersive VR environments but also in the monitor-based study design. This consistency across modalities suggests that the underlying mechanism generalizes across different levels of sensory immersion.

The comparable error patterns observed in the two investigated modalities are theoretically highly relevant. The crucial observation is that the behavioral error pattern itself remained stable across both modalities. This is particularly noteworthy because monitor-based environments provide reduced vestibular and proprioceptive information and generate considerably lower visual flow than immersive VR environments. From a neuroscientific perspective, this is somewhat surprising because continuous self-motion information is generally assumed to be essential for stable PI and grid cell activity [13,34]. The fact that similar effects emerged even in the more abstract screen-based design, which reduced spatial information to a two-dimensional display, similar to maps in this respect, suggests that visual-spatial reference structures may already influence the formation of internal spatial reference frames. This observation supports assumptions proposing that external spatial structures can stabilize internal spatial representations. In line with previous work on cardinal axes and grid-cell-related navigation processes, the present findings suggest that even simple linear cues may systematically affect spatial behavior across different navigation formats [16,17]. This interpretation is consistent with current models of grid cell functioning and PI. Grid cells in the medial entorhinal cortex are characterized by hexagonally organized firing fields that are thought to provide a metric representation of navigable space and support PI processes [8,11]. Previous studies demonstrated that spatially tuned cells are not exclusively active during actual movement through space but also during imagined or visually simulated navigation [59,60]. Doeller et al. [34] provided the first fMRI evidence for grid-cell-like representations in humans and demonstrated that entorhinal hexa-directional activity correlates with spatial memory performance during virtual navigation tasks (see ref. [30]). Consequently, the present findings may indicate that even simplified visual structures are sufficient to influence the neuropsychological structures associated with navigation and cognitive map formation.

The second important result concerns the contextual dependency of environmental reference structures. Notably, the strongest and most consistent evidence across the path integration performance measures was observed for the line-wall contrast. In the VR study, this pattern emerged in distance error, whereas in the monitor-based study it was reflected in the absolute angular error. The experiments demonstrated that the effects of spatial reference cues critically depend on their perceptual and structural properties. Together, these results suggest that the line condition was associated with better performance than the wall condition, although the exact outcome measure showing this effect differed between study designs. Importantly, this comparison reflects differences between two independently recruited samples and should therefore not be interpreted as a direct

causal effect of display medium or immersion. Several additional factors also differed between the two setups, including movement speed, degrees of freedom, visual environment, feedback modality, and boundary transitions, and these may have contributed to the observed differences. The presence of a wall as a cardinal reference structure even tended to impair navigation performance compared to the control condition. At first glance, this finding appears to contradict previous animal studies suggesting that environmental boundaries stabilize grid-cell firing patterns and reduce accumulated PI errors. Hardcastle et al. [13], for example, demonstrated that encounters with environmental boundaries function as an error-correction mechanism for grid cells and contribute to the stabilization of the grid code. Likewise, several studies showed that environmental geometry strongly influences the orientation and symmetry of grid cell activity patterns [14,40]. However, the discrepancy between those findings and the present results can likely be explained by the specific experimental manipulation used in the current studies: After navigating to the first PI position, the wall structure was removed, which resulted in a sudden expansion of the visual field by approximately 180°. This abrupt change in environmental geometry likely disrupted the previously established spatial reference frame and introduced substantial spatial uncertainty. Compared to the raised ground line, which did not restrict the field of view, the wall may thus have functioned as a transient spatial cue rather than a stable environmental anchor, and its removal may have destabilized the internal spatial representation. Such an interpretation aligns with previous findings demonstrating that grid cell activity is highly sensitive to changes in environmental geometry and boundary configurations. This interpretation aligns with previous findings showing that grid-cell activity is sensitive to changes in environmental geometry and boundary configurations [14]. The removal of the wall may therefore have led to a reorganization of the internal spatial map, resulting in increased PI errors. The present findings thus suggest that not every environmental boundary automatically stabilizes navigation performance. Rather, the stability and continuity of spatial reference structures appear to be critical. While stable and persistent environmental cues support metric coding and orientation, abrupt structural changes destabilize ongoing spatial computations. This distinction could provide important mechanistic insight into how environmental boundaries interact with PI systems.

The third major finding concerns the temporal persistence of the observed effects. Crucial for the overall project goal, the visual references—such as the ground-line—were presented only briefly at the beginning of each trial and were subsequently removed before participants performed the actual PI task. This design choice was deliberate, because a continuously visible boundary would have functioned as a permanent spatial reference and could therefore have supported navigation independent of the transient cue presentation. Briefly presenting and then removing the boundary elements was intended to isolate their initial stimulus effects and their potential influence on internal spatial representations. The improved navigation performance, therefore, cannot be explained by continuous visual guidance. Rather, the results suggest that the initial perception of the cardinal axis may have established a persistent internal spatial reference frame that continued to influence navigation after the visual cue had disappeared. Under the assumption that grid-cell activity contributes to this internal reference frame, the findings are consistent with the possibility that boundary-induced stabilization of internal spatial representations persists [8]. The present findings provide behavioral evidence compatible with the assumption by suggesting that even short exposure to cardinal environmental structures may be sufficient to induce a stable internal reference frame that persists after the external cue is no longer visible.

Several limitations of the present studies should be acknowledged. First, some of the statistical analyses were conducted exploratorily, and some effects remained relatively

small. The conclusions require cautious interpretation and independent replication. Second, the present experiments used highly simplified virtual environments that cannot fully represent the complexity of real-world navigation. Third, the monitor-based and VR studies were based on independently recruited samples, so the between-group comparison may also reflect unmeasured individual differences such as spatial ability or prior VR experience. Fourth, the current study provides only indirect behavioral evidence and cannot demonstrate actual grid cell activity. The proposed neuropsychological interpretation, therefore, remains hypothetical and requires validation.

6. Conclusions

The present findings contribute to the growing interdisciplinary field linking cognitive cartography, virtual navigation research, and spatial neuroscience. The results support the idea that external spatial reference structures may systematically influence the neuropsychological processes underlying cognitive map formation. In this context, cardinal axes may represent more than simple orientation aids. Instead, they may interact with neuronal navigational systems responsible for metric spatial coding and PI. Despite these limitations, the study contributes conceptual and methodological insights to the field.

The findings suggest that even minimal and briefly presented spatial reference structures can influence PI performance, although a similar pattern across both setups should be interpreted with caution given additional design differences between the two studies. The most robust evidence in the present study concerned the line–wall contrast rather than a uniform advantage of the line condition across all comparisons. This supports the broader assumption that principles derived from spatial neuroscience could be integrated into future cartographic and navigation-system design in order to improve spatial orientation, cognitive map formation, and navigation performance.

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Data Availability Statement: The original data presented in these studies are openly available on ReSeeD—the central Research Data Management System of Ruhr University Bochum. Part I (contains anonymized data sets, movement data and sample video clips for both experimental studies): <https://doi.org/10.60517/9c592a17-db6b-49d7-be0a-94359b03c243>. Part II (contains the compiled Unity applications for both experimental studies): <https://doi.org/10.60517/c3155fd3-9651-416e-9d2a-9ad795a283ef>.

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Abbreviations

The following abbreviations are used in this manuscript:

fMRI	functional Magnetic Resonance Imaging
GCLR	Grid Cell-Like Representation
HMD	Head-mounted display
M	Mean
max	maximum
min	minimum
n	group size
PI	Path Integration
r	Effect size
SD	Standard Deviation
VR	Virtual Reality
W	Test statistic Wilcoxon

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