

## RESEARCH ARTICLE

# Are Wayfinding Abilities Correlated With Specific Brain Anatomy? An Investigation on Regular Car Drivers Using a Navigational Map in an Unknown Environment

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**Received:** 26 July 2024 | **Revised:** 10 October 2024 | **Accepted:** 5 February 2025

**Funding:** This work was supported by Agence Nationale de la Recherche.

**Keywords:** inter-individual differences | navigational map | spatial cognition | spatial navigation | structural MRI | wayfinding

## ABSTRACT

The ability to navigate spatially in the physical world is a fundamental cognitive skill. This study examines the anatomical correlates of map-assisted wayfinding in an unfamiliar virtual environment using structural magnetic resonance imaging (MRI). Thirty-three participants were required to reach up to seven different locations represented on a navigational map in a simulated environment, while their gazing behavior was recorded, and, in close temporal proximity, the anatomical MRI of their brain was acquired. Significant predictors of wayfinding performance were the volumes of the right hippocampus, left retrosplenial cortex, and posterior cingulate cortex—left inferior frontal gyrus, right superior frontal gyrus, and right cerebellar lobule VIIB. Detailed analyses revealed a dissociation between two clusters of gray matter density in the right hippocampus. Compared with the poorest wayfinders, the best wayfinders exhibited more gray matter density in a cluster located in the right posterior hippocampus but less gray matter density in a cluster located in the anterior section of the hippocampus. In addition, top performers spent more time gazing at the map, highlighting the benefit of using external aids during navigation tasks. Altogether, these results underscore how structural adaptations are associated with spatial navigation performance.

## 1 | Introduction

The ability to navigate spatially in the physical world is a fundamental cognitive skill across the animal kingdom, humans included. These skills are crucial because they enable us to reach destinations that lie beyond our immediate sight and to remember landmarks for future visits. Some even argue that human memory and planning capabilities have evolved directly from our navigation skills (Buzsáki and Moser 2013). If spatial cognition is far more complex and multifactorial than one might anticipate at first glance, purposeful navigation between locations stands as one of the most prevalent real-world demonstrations of

spatial cognition. Navigating from point A to point B is an omnipresent demand in our daily lives, and it has garnered significant attention in research literature over the past half-century. Coined by Lynch (1960), the term “wayfinding” has since been elaborated upon by Golledge, who defines it as “the process of determining and following a path or route between an origin and destination.” (1999, 6).

If you reflect on your recent activities, you will likely discover numerous examples of spatial navigation challenges. Perhaps you met a friend in town, navigated to an unfamiliar pub or your usual meeting spot, escorted your children by bike

to various sports activities, or drove to a new shopping destination. These everyday tasks illustrate the intricate nature of spatial navigation in our lives. Extending the reflection on your activities, you will notice that some wayfinding tasks were remarkably straightforward, like biking to the familiar sports hall you have frequented for years. Yet, others proved much more challenging, such as locating a new restaurant in an unfamiliar city where you are expected to meet a friend, relying solely on a fleeting memory from a map hastily checked on your phone before the battery died. Navigating unfamiliar areas requires a higher cognitive load due to increased demands in route planning, information search, and problem-solving (Arthur and Passini 1992).

In our modern lives, when faced with challenging wayfinding tasks, we often rely on external aids like navigational maps or GPS. In the literature, the focus is mostly set on unaided wayfinding, allowing the study of the sole internal process, as if requiring external aid for wayfinding could be considered cheating. This unassisted wayfinding is also a basis for comparisons between humans and other animals (Wiener et al. 2009, 57). However, exploring aided wayfinding opens the opportunity to delve into a significant portion of everyday spatial navigation situations (Allen 1999). The utilization of external tools or technology to aid in wayfinding prompts inquiries into human-machine interactions. The general human-machine symbiosis framework postulates that our tools are not merely external to users but rather shape the cognitive processes of their users (Navarro 2017a, 2017b; Navarro and Hancock 2023). Applied to wayfinding, external aids are thus expected to modify the unaided wayfinding task, influencing the associated cognitive processes and even shaping those cognitive processes. The nature of these interactions depends on the specific tool and its impact on the task at hand. In this context, we focus on the traditional navigational map (i.e., a scaled bird-eye-view representation of the spatial environment). A simplistic analysis might suggest that individuals only need to engage in “map reading” to navigate effectively. However, a closer examination reveals that the navigational map does not replace the user in the wayfinding task (unlike GPS guidance); instead, it assists the task, following the two main automation philosophies classification (Young et al. 2007; Young and Stanton 2023). Within this classification, inspired by automation in air transportation, tools could either assist or replace the human operator. Navigational maps provide users with an accurate representation of the physical world that is always available. Expanding Wiener’s taxonomy developed for unaided wayfinding to aided wayfinding, a navigational map allows (i) an informed search, leveraging the scaled representation of the environment and the spatial relations between different locations; (ii) target location approximation, based on the scaled depiction of landmarks; and (iii) pathfinding, enabling the planning of a route from the current location to the destination (Wiener et al. 2009). However, it does not provide self-location assistance.

The idea that animals, including humans, construct cognitive maps, a term introduced by Tolman 1948, posits that they develop a mental representation of the layout of the physical environment. These cognitive maps act as internalized blueprints, empowering individuals to navigate and interact with their

surroundings effectively. Rapidly, neuroscientists embarked on extensive studies to explore the neural underpinnings of these cognitive maps. Since the discovery of place cells in the rodent hippocampus (O’Keefe and Dostrovsky 1971), the hippocampus has been regarded as central to cognitive map construction (O’Keefe and Nadel 1978). A groundbreaking study on human navigation skills revealed an enlarged right posterior hippocampus in London taxi drivers who needed to memorize the layout of 25,000 streets and the locations of numerous landmarks to obtain a license (Maguire et al. 2000). Subsequently, this larger hippocampus was linked to active taxi driving, as elderly drivers still engaged in the profession exhibited larger hippocampi compared with their retired counterparts (Woollett et al. 2009). Furthermore, research has shown that London bus drivers, who navigate the city regularly but do not require extensive spatial knowledge like taxi drivers, tend to have smaller posterior hippocampal gray matter density compared with taxi drivers (Maguire et al. 2006). In addition, posterior hippocampal gray matter volume was found to be correlated with years of experience as a taxi driver, indicating a progressive growth of this brain structure with practice (see also Griesbauer et al. 2021 for a review on neurocognitive studies on London taxi drivers; Maguire et al. 2000, 2006).

Although the hippocampus has received significant attention in the study of spatial cognition, several other regions are considered the core of the “navigation network.” In a comprehensive review, these regions were regrouped along three fundamental aspects: spatial coding (in which the *hippocampus* and *entorhinal cortex* are involved, supporting map-like spatial representations), landmark anchoring (in which the *parahippocampal* and *retrosplenial cortex* are implicated, furnishing essential inputs for anchoring cognitive maps to prominent environmental landmarks), and route planning (the *hippocampus* and *entorhinal cortex* aid in generating map-like spatial codes and collaborate with frontal lobe mechanisms to plan routes during navigation) (Epstein et al. 2017). The experimental pieces of evidence of the implication of frontal regions have been recently reviewed, suggesting that the prefrontal cortex is necessary when navigating unfamiliar areas and contemplating alternative routes (Patai and Spiers 2021).

Among the multitude of functions attributed to the prefrontal cortex in the realm of navigation behavior, three stood out as particularly relevant to our study: (i) the involvement of the *lateral prefrontal cortex* in making sequential decisions during path planning, (ii) the role of the *dorsomedial prefrontal cortex* in monitoring progress towards the goal by anticipating key landmarks or junctions, as well as tracking self-motion relative to a prior location, and (iii) the contribution of the *dorsolateral prefrontal cortex* to support active decision-making at junctions (Patai and Spiers 2021).

In addition to the brain regions typically linked to spatial navigation, we also consider another brain area, linked with a process that might play a role in our map-aided wayfinding task. Visual divergent thinking, a central component of visual creativity, involves the ability to explore numerous visual concepts. As the wayfinding task used in our study involves visually exploring a map and envisioning several paths to the

next location, this process might be implicated and supported by a network of areas encompassing lobules VI, VIIIB, Crus I, and Crus II of the cerebellum (Gao et al. 2020). Furthermore, the cerebellum, traditionally associated with motor coordination, has recently been implicated outside the motor context (Ivry and Baldo 1992; King et al. 2019). More specifically, recent research has highlighted the role of the cerebellum's posterior lobe in supporting cognitive and emotional processes, making it particularly intriguing in the context of our study (Schmahmann 2019; Stoodley and Schmahmann 2018). *Lobule VI*, *Crus I*, and *VIIIB* were activated by executive functions such as planning, organizing, and strategy formation (see Schmahmann 2019 for a review; Stoodley et al. 2012; Stoodley and Schmahmann 2009) and *lobule VI* (Stoodley and Schmahmann 2009) and *Crus II* (Stoodley et al. 2012) were found active for spatial processing such as mental rotation tasks (and see Guell et al. 2018). Even more recently, the role of the cerebellum in human spatial navigation has been suggested, potentially in interaction with subcortical or cortical structures such as the hippocampus (Li et al. 2021; Rochefort et al. 2013). Structural brain differences between participants, due to innate and/or practice of navigational skills (Kanai and Rees 2011; May 2011), were therefore hypothesized in the brain regions previously associated with wayfinding and visual divergent thinking.

Among the many experimental set-ups utilized by researchers, the investigation of spatial navigation during driving holds particular significance. This is due to its provision of large-scale environments and its status as a commonplace activity in modern societies (Lee 2008). Despite its commonality and perceived simplicity, car driving entails a multitude of subtasks that engage various cognitive processes (Spiers and Maguire 2007; Walker et al. 2015). Researchers have proposed a framework for understanding the neural underpinnings of car driving across three levels of cognitive control (Navarro et al. 2018), those being subject to assistance technologies advancements (Navarro and Reynaud 2023). In a study focusing on spatial navigation during driving, licensed London taxi drivers participated in a simulated car driving experiment where they were tasked with reaching multiple destinations unaided. Hippocampal activity was observed solely during the planning phase of a route to a novel destination, rather than throughout the entirety of the navigation task. Moreover, findings revealed the involvement of the retrosplenial cortex and prefrontal cortex regions during navigation tasks, aligning with the core network of brain regions associated with spatial navigation (Spiers and Maguire 2006). In another driving simulated experiment, with route planning done (and corrected by the experimenter before the actual drive), drivers' visuospatial abilities and memory were linked to both their wayfinding performances and how well participants drove (Bryden et al. 2023). Furthermore, real and simulated driving elicited similar wayfinding performances (Cochran and Dickerson 2019).

A critical aspect of wayfinding during driving is understanding how drivers allocate their visual attention between the road and external aids, such as navigational maps. Although driving, the visual demands of maintaining road safety limit the time available to glance at a map, as drivers must focus on the road to steer effectively (Lappi and Mole 2018; Navarro et al. 2020;

Shinar 2008). This creates a unique challenge, as consulting a map while driving disrupts the continuous visual scanning required for safe vehicle operation (Navarro et al. 2021). Despite the widespread use of navigation aids, there is limited understanding of how map use during driving impacts wayfinding performance. Looking at the map while driving would necessarily interfere with the driving task and compel the driver to halt for a more extended examination.

In the reported experiment, participants were tasked with navigating a virtual environment that was entirely unfamiliar to them before the experiment. Consequently, they did not rely on long-term spatial memory for wayfinding. Instead, their challenge was to explore the map of the virtual environment, which was continuously accessible to them in a bird's eye view. Wayfinding and spatial navigation performance in this new and complex urban environment should differ depending on the individual's cognitive abilities for such tasks. It was hypothesized that high performances would be correlated with structural markers in the key regions involved during wayfinding, spatial navigation, and visual divergent thinking. In addition to brain morphometry analysis, participants' visual interactions with the map were investigated. Top performers were expected to be more efficient at the wayfinding task, and faster at building a cognitive map and thus they should spend less time gazing at the map representing the virtual environment than poorer performers.

## 2 | Methods

### 2.1 | Participants

Thirty-three (19 female) participants aged between 21 and 36 years old (mean age:  $23.9 \pm 3.0$  years old) took part in the experiment. All were licensed drivers with an average driving experience of  $5.0 \pm 1.8$  years and a declared number of driven kilometers per year of  $7591 \pm 6326$ . Video gaming experience was also collected through self-reported weekly hours of video gaming per week (mean:  $6.3 \pm 9.0$  h). Detailed demographic data can be found in the [Supporting Information](#).

### 2.2 | Equipment

#### 2.2.1 | Magnetic Resonance Imaging (MRI) Acquisition

T1-weighted (T1w) anatomical images were acquired with the following parameters: repetition time (TR) of 3000 ms, echo time (TE) of 2.93 ms, flip angle of  $8^\circ$ , a voxel size of  $0.8 \times 0.8 \times 0.8$  mm, and a matrix size of  $280 \times 320$ , acquiring 224 sagittal slices. These scans were conducted using a 3-Tesla MR scanner (MAGNETOM Prisma, Siemens Healthcare, Erlangen, Germany) fitted with a 64-channel head coil. The raw imaging data were stored in DICOM format and subsequently converted to NIfTI format utilizing the dcm2nii software from Chris Rorden's laboratory (<https://github.com/rordenlab>). Quality assurance checks were performed by an experienced neuroradiologist to ensure the absence of significant artifacts or incidental brain abnormalities.





**FIGURE 1** | Driving simulation setup and representation of the three main visual areas of interest (AOIs).

### 2.2.2 | Driving Simulation

The experiment utilized a fixed-base simulator outfitted with an automatic gearbox, offering a horizontal field of view spanning approximately  $145^\circ$  across three computer screens. A traditional analog speedometer was conveniently positioned at the bottom center of the middle screen for easy reference. In addition to the visual setup, the experimental rig included an adjustable seat (JCL Sim Racing), a steering wheel equipped with force feedback, and responsive accelerator and brake pedals (Logitech G27). The driving simulation software powering the experience was crafted by the University of Sherbrooke (refer to Navarro et al. 2019 for comprehensive insights). The experimental setup was completed by a Garmin VIRB recording camera, strategically positioned to capture the driver's gaze on various points of interest: the screen (i.e., simulated driving environment), the map (printed and available at all times on the dashboard), locations prints (i.e., screenshots of the different locations to be visited during the simulated drive), the remaining gaze fixations were grouped into a “other elements” category (see Figure 1).



**FIGURE 2** | Map of the simulated driving environment, as presented and available all the time to participants. The labels, in red, were kept in French as used for the experiment. The top red point “Départ” indicates the starting location and seven different locations were pinpointed.

## 2.3 | Procedure

All experimental protocols adhered to the ethical standards outlined in the 1964 Declaration of Helsinki. Approval for the study was granted by the French Ethics Committees (reference number 2018-A00734-51). Participants were recruited randomly through advertisements posted on various social media platforms and at the University of Lyon 2. Two weeks before their scheduled MRI session, participants provided informed consent to participate in the study and underwent eligibility assessments conducted by a medical professional. Subsequently, participants attended the MRI session at Lyon's Neuroimaging Department (CERMEP, Lyon France). The driving simulation session was conducted at the University of Lyon 2 within a fortnight after the MRI session.

The MRI session consisted of an anatomical scan of about 8 min, during which the participant was simply asked to remain as still as possible.

The driving simulation session was initiated by a familiarization drive that lasted about 10 min to ensure that the participants handled the driving simulator properly and got used to the simulated environment. Then, the experimental task was undertaken. The simulated environment was created for the experiment and was not a reproduction of an existing city, although inspired by the historic downtown area of Valenciennes, France. The streets consisted of two-lane roads with opposing traffic lanes, but no other vehicles were present.

Participants were instructed that they would be required to navigate in an unknown environment based on a map with a starting point and seven different locations pinpointed to visit. Before that, they would have two minutes to look at the city map to offer them the possibility to identify landmarks and recognize the starting point of the driving simulation. Then, they were instructed to visit as many locations as possible within 15 min while adhering to traffic regulations. The next location to visit will be displayed on the driving screen as soon as a given location is reached and immediately after the starting point.

The experiment itself started with participants being presented with the map representing the new driving environment from a bird's eye view (Figure 2) two minutes before the beginning of the driving simulation. During those two minutes, they could also look at a screenshot of different locations pinpointed on the map (a print per location). Both the map and the "location prints" would remain available to participants for the complete duration of the experiment. The map detailed the navigable streets (all usable in both directions) and the locations of seven landmarks: park, museum, shopping center, hospital, cathedral, gas station, and swimming pool (Figure 2).

The task ended either when participants reached the final landmark or after 15 min, at which point the experimenter stopped the simulation. Participants were then asked to complete the NASA-TLX to evaluate the perceived workload during the task (Hart and Staveland 1988). In addition, they were asked to rate their perceived performance on a scale from 0 to 10, with 10

representing the best performance and 0 the worst performance possible. Overall, each simulated driving session lasted about forty-five minutes.

## 2.4 | Data Analysis

### 2.4.1 | Region-Based Morphometry Analysis

We performed automatic segmentations of structural images with an online tool based on a multi-atlas patch-based label fusion segmentation approach (Coupé et al. 2011; Manjón and Coupé 2016). Vol2Brain (Manjón et al. 2022) (available online at <https://volbrain.net/services/vol2Brain>) was used to parcel the brain into 135 brain structures, on different scales. This pipeline operates on macro levels to determine, for example, the Gray Matter volume or the ventricles volumes, but also on a more detailed level to assess specific brain areas as defined by the NeuroMorphometrics standards (<http://neuromorphometrics.com>). Normalized volumes were computed for each brain structure. Ceres (<https://volbrain.net/services/CERES>) was used to perform parcellation of the cerebellum into lobules and cruces, according to the cerebellum atlas defined in (Park et al. 2014). The volumes were computed for 12 sub-parts of the cerebellum (lobules I to X + Crus I and II), in each hemisphere.

To assess the structural regions that might be related to wayfinding performance, we chose to linearly regress the wayfinding score against variables measuring normalized volumes (related to total intracranial volume [TIV]) of cortical, subcortical, and cerebellar regions, together with demographic variables. This led us to select the following brain regions:

**Cortical and subcortical regions:** These areas consist of areas from the core spatial navigation network: hippocampus, parahippocampal gyrus, retrosplenial area—posterior cingulate gyrus (PCgG), entorhinal area (Ent) on both hemispheres (8 measures). Then, we also included lateral, dorsomedial and dorsolateral prefrontal regions previously associated with spatial navigation consisting of thirteen sub-regions (frontal pole, superior frontal gyrus [SFG], middle frontal gyrus, opercular part of the inferior frontal gyrus, orbital part of the inferior frontal gyrus, triangular part of the inferior frontal gyrus [TrIFG], precentral gyrus [PrG], superior frontal gyrus medial segment [MSFG], supplementary motor cortex, medial frontal cortex, gyrus rectus, subcallosal area, precentral gyrus medial segment [MPrG]) on both hemispheres (26 measures).

**Cerebellar regions:** Because the posterior part of the cerebellum could also be implied in wayfinding, we also assessed the potential link between the navigation performance and the bilateral volumes (normalized with TIV): Crus 1, Crus 2, lobule VI, lobule VIIA, lobule VIIIA, lobule VIIIB, and lobule IX (14 measures).

Several variables known to be able to influence navigation skills have also been included as covariates in the regression models. On top of the classical age and gender variables (Munion et al. 2019; van der Ham and Claessen 2020; Weisberg et al. 2019), video gaming experience (McLaren-Gradinaru

et al. 2023; Yavuz et al. 2024), self-reported driving experience and self-reported driving frequency (Lajunen et al. 2022) were also included as covariates in the regression models, forming 5 additional measures.

Due to the great number of variables and the potential multicollinearity between them, we performed a partial least squares regression (Abdi 2010; Wold et al. 1993) for predicting the wayfinding performances with the R package *mdatools* 0.14.2 (Kucheryavskiy 2020). PLS regression is a linear multivariate regression that orthogonalizes the predictors into latent independent components. This projection to a latent structure is used to predict the dependent variable. The model's predictive power is then assessed via cross-validation (here a leave-one-out method) and statistics associated with regression coefficients are computed through a jackknife procedure (Anderssen et al. 2006; Martens and Martens 2000). Coefficients with an absolute value statistically different from 0 were selected to be potentially predictive of the performance, in a PLS-SIG strategy (see, for example, Afanador et al. 2013). However, as the estimation of coefficients can sometimes be sensitive to noise, and as we also wanted to have an idea of the importance of each of these predictive variables, we doubled the PLS-SIG strategy with another strategy for variable selection: the Variable Importance Projection method—VIP scores (Wold et al. 1993, 2001). This method enables understanding the variables that predict the most variation in both dependent and independent variables. Their scores allow the selection of important variables and their ranking according to their importance (PLS-VIP strategy). Variables with a VIP score above a certain threshold are considered important predictors. The threshold is theoretically fixed to 1, but in practice, many studies have used a threshold above this value (see, for example, Chong and Jun 2005; Modlich et al. 2005; Pérez-Enciso and Tenenhaus 2003). Here the criterion cut-off was arbitrarily fixed to  $VIP \geq 1.4$ , as it allowed to have a reasonable number of predictors in all regressions performed. The combination of more than a single selection procedure was found to be an efficient selection strategy as they can all be sensitive to noise (Andries et al. 2013; Tran et al. 2014).

#### 2.4.2 | Driving Simulation

Wayfinding performance was assessed through the *total number of locations* reached and was recorded for each participant from 0 (the participant never reached the first location within the 15 min allocated) to 7 (all seven locations were reached by the participant within the 15 min allocated).

The videos captured from the camera were manually annotated every second to assess the driver's visual behaviors. The *percentage of time* spent gazing at the screen, the map, the location prints, and the other elements was computed. The *number of visits* to those elements was also computed.

A subjective *workload score* (NASA TLX) and a *performance score* were computed.

### 3 | Results

#### 3.1 | Behavioral Data

##### 3.1.1 | Wayfinding Performance

On average, the participants reached  $4.39 \pm 1.78$  different locations out of the seven available in the simulated drive. Figure 3 represents a plot of the distribution of the total number of locations reached.

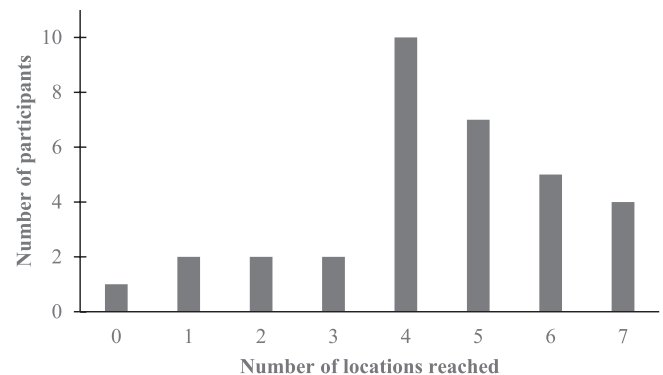
##### 3.1.2 | Wayfinding Performance and Visual Behaviors

The relationships between wayfinding performances (i.e., the total number of locations reached) and visual behaviors (i.e., percentage of time spent gazing at the different AOIs) were investigated using Pearson's correlations (see Figure 4 for the scatterplots).

Both location prints and other location AOIs were significantly gazed less along with wayfinding performances increase,  $r(32) = -0.58$ ,  $p < 0.001$ ,  $BF_{10} = 79.5$  and  $r(32) = -0.48$ ,  $p = 0.01$ ,  $BF_{10} = 9.6$  respectively. An insignificant trend was observed for the percentage of time spent gazing at the map,  $r(32) = 0.317$ ,  $p = 0.08$ ,  $BF_{10} = 0.98$ . The time spent gazing at the screen was not significantly correlated to the wayfinding performances,  $r(32) = -0.19$ ,  $p = 0.30$ ,  $BF_{01} = 2.7$ .

To further investigate differences between participants, they were divided into two groups according to a median split based on the total number of locations reached (see Figure 5 for resulting rainclouds and boxplots). An analysis of variance (ANOVA) with the AOI gazed as the repeated measure factor (screen, map, location prints, and other) and wayfinding performance-based groups (below-median performers and above-median performers) as between participants factor, showed a significant interaction between those two factors ( $F(3, 90) = 7.60$ ,  $p < 0.001$ ,  $\eta^2 = 0.20$ ). Holm post hoc test revealed a significant difference between below- and above-median performers for the screen and map AOIs ( $p < 0.05$ ), with above-median performers gazing more at the map (5.4% on the average) and less at the screen (7.5% on the average) than below-median performers (Figure 5).

To complement the percentage of time spent looking at the different AOIs, the number of visits to the different AOIs was



**FIGURE 3** | Distribution of the total number of locations reached from 0 (no location reached) to 7 (all locations reached).

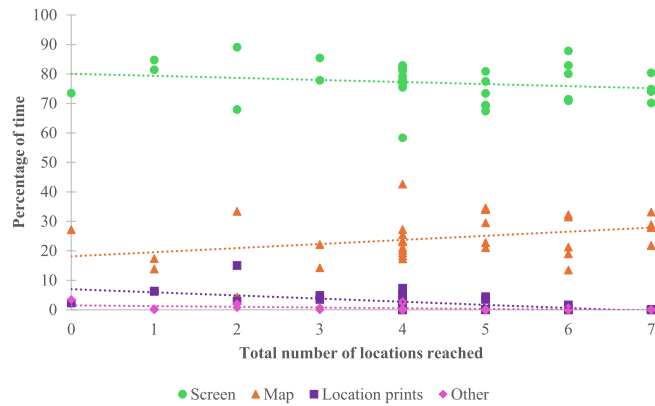


analyzed. The number of visits at the map AOI was not significantly correlated to the wayfinding performances,  $r(32)=0.13$ ,  $p=0.23$ ,  $BF_{01}=2.3$ . Similarly, no significant correlations between the number of visits and the wayfinding performances were recorded for the screen and other elements ( $r(32)=0.00$ ,  $p=0.99$ ,  $BF_{01}=4.5$  and  $r(32)=-0.35$ ,  $p=0.05$ ,  $BF_{01}=0.7$ , respectively). The number of visits to the location prints was negatively correlated with wayfinding performances,  $r(32)=-0.58$ ,  $p<0.001$ ,  $BF_{10}=79.5$ .

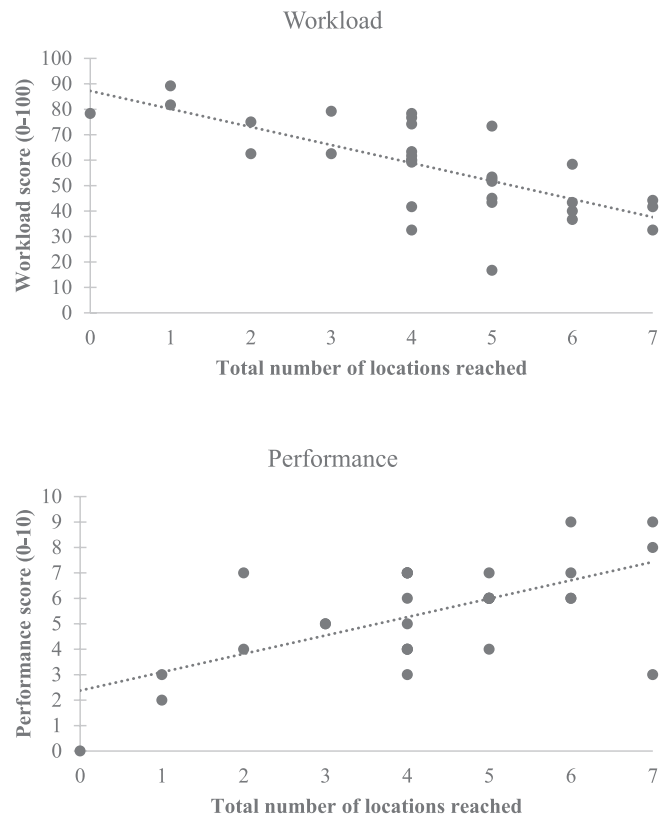
### 3.1.3 | Wayfinding Performance and Subjective Assessments

The relationships between wayfinding performances (i.e., total number of locations reached) and subjective assessments (i.e., workload and performance) were investigated using Pearson's correlations (Figure 6).

The subjective workload was significantly negatively correlated with wayfinding performances,  $r(31)=-0.71$ ,  $p<0.001$ ,

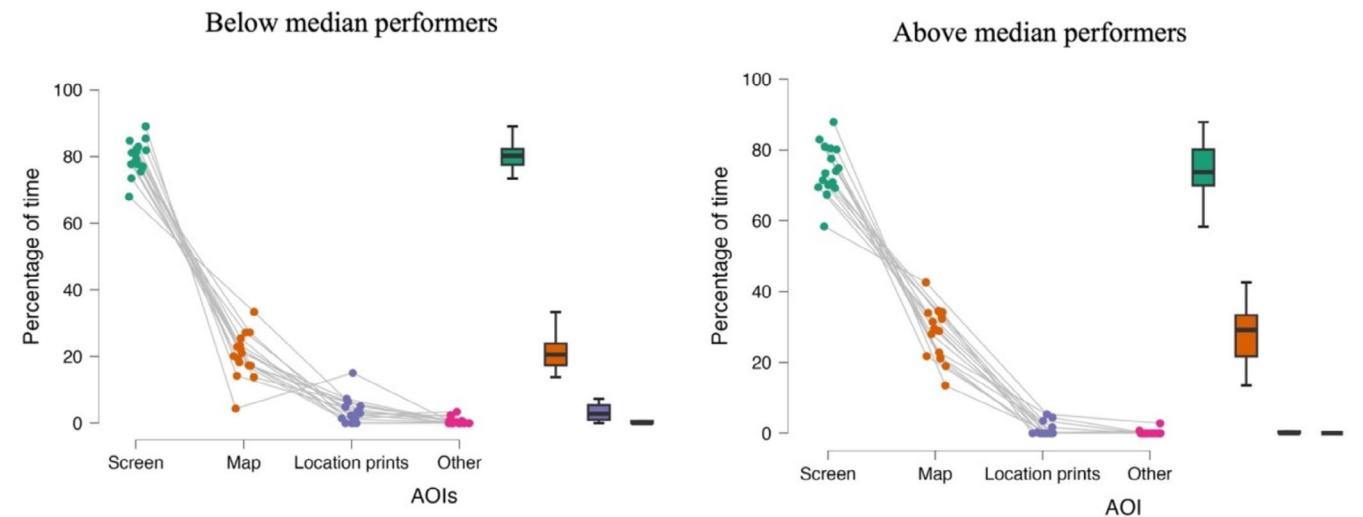


**FIGURE 4** | Scatterplots of the total number of locations reached and the percentage of time spent looking at the AOIs (screen, map, location prints, and others).



**FIGURE 6** | Scatterplots of the total number of locations reached along with subjective workload (top) and subjective performance (bottom).

$BF_{10}=2869.3$ , whereas subjective performance was significantly positively correlated with wayfinding performances,  $r(31)=0.63$ ,  $p<0.001$ ,  $BF_{10}=204.1$ .



**FIGURE 5** | Rainclouds and boxplots of the percentage of time spent at gazing the different AOIs for below-median performers (left) and above-median performers (right).

**TABLE 1** | Predictors with a significant (or trendily significant) coefficient for the PLS regression of wayfinding performance over cerebrum regions and demographic variables.

	Estimated	Std. err.	<i>t</i>	<i>p</i>	2.5%	97.5%
<i>Hippocampus.right</i>	−16.906	6.008	−2.785	0.009 *	−29.143	−4.669
<i>TrIFG.left</i>	11.933	4.612	2.541	0.016 *	2.539	21.328
<i>PCgG.left</i>	11.193	4.747	2.319	0.027 *	1.524	20.862
<i>PrG.right</i>	3.178	1.412	2.203	0.035 *	0.302	6.055
<i>SFG.right</i>	3.011	1.483	1.995	0.055 †	−0.010	6.031
<i>Driving exp.</i>	0.180	0.090	1.963	0.058 †	−0.004	0.363
<i>Gender</i>	0.616	0.321	1.902	0.066 †	−0.037	1.270

Note: \*  $p < 0.05$ , †  $p < 0.1$ . 95% confidence intervals of the estimate are given in the “2.5%” and “97.5%” columns.

### 3.2 | Brain Structural Data

#### 3.2.1 | Wayfinding Performances in Cortical and Subcortical Regions

A model with a structure of two latent components was found ( $R^2=0.825$ ) for the 39 standardized predictors included. For the PLS-SIG strategy, the regression coefficients in the original variable space were estimated (jackknife procedure, DoF = 32). According to this selection step, the following variables were found predictive of the wayfinding performance (i.e., their value differed significantly from the 0 value in a  $t$ -test with  $p < 0.05$ ): *Hippocampus.right*, *PCgG.left*, *TrIFG.left*, *PrG.right*. Close to the statistical threshold, the following variables were found tendentially significant: *SFG.right*, *Driving experience*, *Gender*. Estimated coefficients as well as confidence intervals at  $\alpha = 0.05$  and associated  $p$  values are reported in Table 1 (the full table can be found in Table S2).

This first step into variable selection was confirmed by the PLS-VIP section procedure, computing the VIP scores for each predictor. Retaining all predictors with a VIP score at, or greater than 1.4, the following variables were considered as important for wayfinding performance, ranked in importance order as represented in Table 2 (see Table S3 for all scores): *TrIFG.left*,

**TABLE 2** | Predictors with a VIP score above the selected threshold for the PLS regression of wayfinding performance over cerebrum regions and demographic variables ordered by variable importance criterion VIP.

	VIP scores
<i>TrIFG.left</i>	2.03
<i>Hippocampus.right</i>	1.93
<i>Gender</i>	1.62
<i>PCgG.left</i>	1.53
<i>Driving exp.</i>	1.51
<i>SFG.right</i>	1.47
<i>PrG.right</i>	1.40

*Hippocampus.right*, *Gender*, *PCgG.left*, *Driving exp.*, *SFG.right*, *PrG.right*.

All these variables were found to be statistically significant (or near-significant) by the PLS-beta strategy, so this list of seven predictors of wayfinding performance was considered final.

Because enlarged right posterior hippocampi were previously reported as associated with better navigation skills (Maguire et al. 2000; Woollett et al. 2009), finer-grain analyses were undertaken on the right hippocampus. For an exploration of the gray matter density unconstrained by the automatic frontiers imposed by the RBM methodology, we performed a voxel-based morphometry analysis with the CAT12 toolbox to assess voxel-by-voxel gray matter density (Gaser et al. 2023). For this, the T1-weighted MRI structural images were segmented, spatially registered with standard tissue probability maps, modulated, and spatially smoothed with a Gaussian filter (FWHM = 12 mm). The TIV was computed and added as a covariate in the statistical model (Malone et al. 2015) operating on the pre-processed images. Below- and above-median performers groups were compared with a two-sample  $t$ -test. The resulting contrast images were masked by atlas-defined hippocampal regions of interest. The first contrast described the voxels, within the hippocampi, where above-median performers have an increased gray matter density compared with below-median performers. This led to a single cluster ( $k=138$ ) centered on [26; −33; −9] in the MNI space ( $p < 0.002$ ) inside the posterior part of the right hippocampus. The reverse contrast (below-median > above-median performers) led to a small cluster ( $k=20$ ) centered around [38; −24; −15] in the MNI space ( $p < 0.01$ ), within the anterior part of the right hippocampus. The two statistical maps were overlaid with Mricrogl on an MNI152 glass template presented in Figure 7 (Rorden and Brett 2000).

#### 3.2.2 | Wayfinding Performances in the Cerebellum

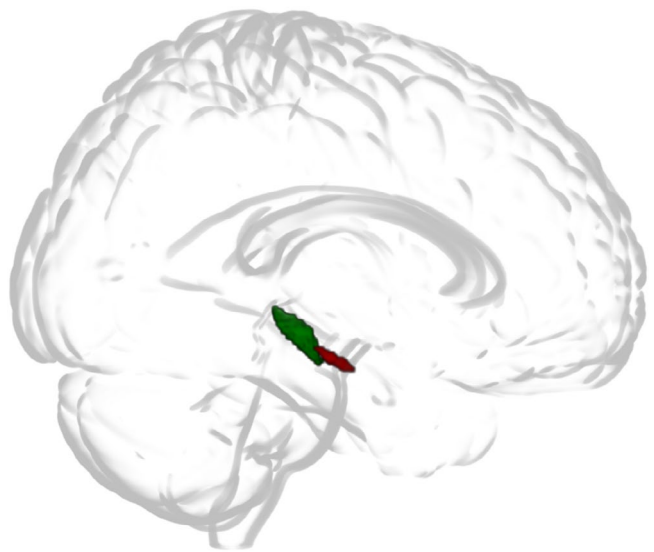
Predictors in the cerebellum, complimented with the demographic variables (19 predictors) were found to project best on a single-component model ( $R^2=0.355$ ). The PLS-SIG strategy indicated that the following predictors had an impact on the wayfinding performance: *VIIB.left*, *VIIB.Right*, *Crus.I.left*, *Crus.I.right*, *Crus.II.left*, *Crus.II.right*, *VIIIA.left*, *VIIIB.left*,



*Gender*. *Video gaming experience* was found to be tendentially significant ( $p < 0.055$ ). Estimations for these predictors are reported in Table 3 (the full table can be found in Table S4).

VIP scores indicated that the following predictors could be important for the wayfinding performance: *VIIB.right*, and *VIIB.left*, as reported in Table 4 (a full list can be found in Table S5).

Combining both selection methods, only two variables remained: *VIIB.right* and *VIIB.left*. Variables *Crus.I.left*, *Crus.II.left*, and *Crus.II.right* were nonetheless close to selection.



**FIGURE 7** | Gray matter density in the right hippocampus. The green cluster corresponds to the first contrast (above-median > below-median performers). The red cluster corresponds to the reverse contrast.

**TABLE 3** | Predictors with a significant (or trendily significant) coefficient for the PLS regression of wayfinding performance over cerebellar regions and demographic variables.

	Estimated	Std. err.	<i>t</i>	<i>p</i>	2.5%	97.5%
VIIB.left	−2.747	0.703	−3.914	0.000 *	−4.180	−1.314
Crus.II.left	−1.330	0.363	−3.676	0.001 *	−2.068	−0.591
VIIB.right	−3.623	1.108	−3.274	0.003 *	−5.880	−1.366
Crus.II.right	−0.972	0.319	−3.050	0.005 *	−1.622	−0.321
Crus.I.left	−1.113	0.383	−2.912	0.007	−1.894	−0.333
VIIIA.left	−1.046	0.404	−2.598	0.014 *	−1.869	−0.223
VIIIB.left	−2.508	0.988	−2.545	0.016	−4.521	−0.494
Crus.I.right	−3.360	1.349	−2.497	0.018 *	−6.108	−0.611
Gender	0.222	0.096	2.312	0.027 *	0.026	0.417
Video-game exp.	0.011	0.005	2.000	0.054 †	0.000	0.021

\*  $p < 0.05$ , †  $p < 0.1$ . 95% confidence intervals of the estimate are given in the “2.5%” and “97.5%” columns.

**TABLE 4** | Predictors with a VIP score above the selected threshold for the PLS regression of wayfinding performance over cerebellum regions and demographic variables, ordered by variable importance criterion VIP.

	VIP score
VIIB.right	1.67
VIIB.left	1.40

## 4 | Discussion

A map-assisted wayfinding task in an unfamiliar virtual environment was conducted following a full brain MRI structural scan of the participants. The wayfinding performances varied widely, with some participants failing to reach any location while others reached all seven within the allotted time. Notably, the top performers spent more time gazing at the navigational map compared with the lower performers. The normalized volumes of the right hippocampus, the left PCgG, comprising the retrosplenial cortex, the right PrG, two frontal regions—the left inferior frontal gyrus (TrIFG) and the right SFG—and bilateral lobules VIIB in the posterior lobe of the cerebellum showed significant correlations with wayfinding performance. These findings support the hypothesis that these brain regions, known to contribute to spatial navigation thanks to previous functional MRI studies, exhibit structural changes due to cerebral plasticity. This underscores the role of these areas not only in spatial navigation but also in the long-term structural adaptations of the brain.

The key decision to leave participants to work their way into the different locations in an unknown environment was made. Because the environment was unknown before the experiment, participants could not use previous knowledge related to that specific environment. In other words, they had to find their way into the environment from scratch. They were offered two minutes before the start of the driving simulation to study the map of the environment but without knowing which location they would have to reach at first and in which order

the different locations would have to be visited. It was thus impossible to anticipate the future path, especially with such a limited time.

The only thing that participants could do was to familiarize themselves with the environment (i.e., initiate building a cognitive map) and with the different locations (i.e., initiate adding landmarks to their cognitive map). It was anticipated that participants with stronger spatial navigation skills would construct more accurate cognitive maps during this time, leading to better performance in the subsequent wayfinding tasks (up to seven consecutive tasks). Although under debate (Weisberg and Ekstrom 2021), prior research repeatedly linked posterior hippocampal volume with navigation abilities (Griesbauer et al. 2021). If the posterior hippocampal volume is indeed associated with navigation abilities, our participants with larger posterior hippocampi should demonstrate superior wayfinding performance. This link was not supported by our initial findings: normalized volume of the left hippocampus was not significantly correlated with wayfinding performances, and the enlarged right hippocampus was associated with poorer wayfinding performances, as the coefficient was estimated negative. Finer gain analyses of the right hippocampus revealed a dissociation between two clusters of gray matter density. Compared with below-median performers, above-median wayfinding performers exhibited more gray matter density in a cluster located in the right posterior hippocampus but less gray matter density in a cluster located in the anterior section of the hippocampus.

The role of the hippocampus in wayfinding using a navigational map among regular drivers warrants closer examination. The right posterior hippocampus has consistently been identified as crucial for spatial navigation (see Griesbauer et al. 2021, for a recent review). The right posterior hippocampus is also known to be essential for accurate wayfinding (Hartley et al. 2003), predominantly engaged during the planning phase of a route to a novel destination, rather than throughout the entire navigation task (Spiers and Maguire 2006). Our results align with these findings. We observed that the gray matter density in a cluster located in the posterior part of the right hippocampus correlates significantly with wayfinding performance. This reinforces the idea that the right posterior hippocampus is crucial including in map-assisted wayfinding tasks. This perspective is not consistent with studies showing no significant differences in the posterior right hippocampal volume related to navigation abilities among young adults, who exhibit a wide range of navigation skills (Weisberg et al. 2019) or route sequencing skills (Clark et al. 2020), both studies featuring substantial sample sizes drawn from the general population.

Higher gray matter density was observed in a cluster located in the anterior right hippocampus for the below-median performers as compared with above-median performers, a difference also unobserved by Weisberg et al. (2019). Again, our findings resonate more with the famous studies of London taxi drivers which observed larger anterior hippocampi for regular drivers than London taxi drivers and for inexperienced than experienced London taxi drivers (Maguire et al. 2000, 2006). Unlike the posterior hippocampus, the anterior hippocampus has not garnered as much research attention in the spatial navigation field. The current findings suggest that a higher gray matter

density in the right anterior hippocampus might be detrimental to wayfinding performance.

This is an intriguing result that is challenging to interpret, particularly because learning the layout of a new virtual environment has been linked to increased functional activity in the anterior hippocampus (Wolbers and Büchel 2005). In addition, the anterior hippocampus is known to be involved in encoding tasks, such as determining relative landmark positions (see Poppenk et al. 2013, for a review). Precisely a task that our participants had to perform; nonetheless, top performers were associated with thinner anterior right hippocampi. A tentative explanation could be that the anterior hippocampus is engaged in creating global spatial representations (Poppenk et al. 2013), an ability that might have been detrimental to performance in our protocol. In our study, the exact position of the location needed to be precisely reached to engage in the subsequent wayfinding task. Still, the negative correlation between the anterior hippocampus and wayfinding performance raises questions about its role in encoding and integrating new spatial information during the initial learning stages of unfamiliar environments.

Altogether, the reported findings contribute to the ongoing debate about the relationship between hippocampal structure and navigation ability (Weisberg and Ekstrom 2021). Three hypotheses have been proposed to explain conflicting results: (i) hippocampal structure correlates with navigation skills, but only for individuals with either exceptionally high or exceptionally low abilities; (ii) hippocampal structure is specifically linked to certain navigational skills, in particular, allocentric navigation; and (iii) hippocampal structure alone does not adequately measure the multifaceted nature of human spatial navigation (Weisberg and Ekstrom 2021). Our findings directly argue against hypotheses (i) and (ii). First, right hippocampus gray matter density was found related to wayfinding performances for individuals without exceptionally high or exceptionally low navigational abilities. This rules out the rationale that hippocampus structure is only associated with individuals with exceptional navigational abilities. Second, hippocampal structure was found related to wayfinding performances in a map-assisted wayfinding task implying navigation with numerous changes in directions and positions in the simulated environment. This rules out the rationale that hippocampus structure is specifically associated with allocentric navigation. Conversely, our findings support hypothesis (iii), with a few brain structures associated with wayfinding performances rather than the hippocampus exclusively.

Furthermore, our data suggest some alternative explanations. Our findings showed opposite relationships between wayfinding performances and the right hippocampus structure, in an anterior and a posterior cluster of gray matter density. This finding suggests several potential implications that warrant further exploration. First, considering the whole hippocampus may well be a source of confusion as distinct regions of that cerebral structure prove to have opposite links with wayfinding performances. Second, the nature of the navigational task at hand may have a critical importance on the associated cerebral bases, including the hippocampus. We used a natural task engaging actual wayfinding and associated traveling in a large-scale virtual environment. Some other tasks might mostly engage memory processes associated with spatial

information. For instance, Weisberg et al. (2019) used a form of spatial memory task, where participants are required to learn a route (without the possibility of making any mistake) and then recall the direction of the buildings or directly rebuild the environment in a bird's eye view. This task is highly relevant to investigating cognitive maps, as learning a route is directly associated with the construction of a cognitive map and the ability to recall spatial relationships in that cognitive map. However, the cognitive processes and brain regions engaged may not be the same as the ones engaged during wayfinding, a task requiring navigating through the environment to reach different locations. Third, because the posterior part of the right hippocampus structure supports above-median wayfinding performances, our findings support the rationale that this hippocampal location is key for route planning. Due to the high number of roads and intersections, our task required a lot of route planning and replanning along the way to the different locations. This is consistent with previous observations made during specific route planning periods (Spiers and Maguire 2006). Finally, the discrepancy in the hippocampal structure between regular drivers (see Weisberg and Ekstrom 2021, for a review), and London taxi drivers (see Griesbauer et al. 2021, for a review) may be partially explained by the exceptional spatial abilities of taxi drivers. Their extensive training allows them to mentally navigate London's complex street layout with a level of detail akin to physically performing a wayfinding task, a skill that is less developed in regular drivers.

Altogether, it appears that hippocampal structure may not be the only cerebral structure involved in spatial navigation across all types of expertise and forms of spatial navigation tasks. Our results support the notion that the right posterior hippocampus is a key brain region for self-location and wayfinding using a navigational map. Intriguingly, the opposite was observed for a more anterior hippocampus cluster: the larger the right anterior hippocampus was, the poorer the navigation skills were. This counterintuitive finding highlights the need for further research to understand the distinct roles of different hippocampal regions in spatial navigation, potentially in interaction with other brain structures.

Apart from the hippocampus, the brain structures associated with the best wayfinding performances align with previously reported functional structures in driving simulation (Spiers and Maguire 2006). This alignment is particularly significant as it underscores the structural specificity of wayfinding tasks, extending previous functional observations to inter-individual differences in brain volume. In addition, it highlights the consistent relevance of the retrosplenial cortex across various spatial navigation tasks (map-based wayfinding on top of wayfinding based on the memorized layout of London) and population (regular drivers on top of London taxi drivers). The retrosplenial cortex proves crucial both with and without the use of a navigational map, as well as in known and unknown environments (Hartley et al. 2003). In the context of our experiment, it could be hypothesized that the retrosplenial cortex is beneficial in its two broad functional categories: (i) translating between perspectives, specifically converting allocentric positions and orientations from map reading to egocentric first-person viewpoint changes through self-motion tracking, and (ii) comparing perceptual

input with memory, which involves matching perceptual input about the current location with the memory of the targeted location (Alexander et al. 2023; see also Mitchell et al. 2018).

Conversely, the cortical volume of other regions within the core spatial navigation network did not show a significant relationship with wayfinding performances, suggesting that these areas may not play as pivotal a role in map-aided wayfinding, at least in terms of brain structures. Specifically, the volumes of the parahippocampal and entorhinal regions were not found to correlate with wayfinding performance in our study. This structural investigation did not replicate the functional activations of these regions observed during spatial navigation tasks. Although these regions are known to support map-like spatial representations, provide essential inputs for anchoring cognitive maps to prominent environmental landmarks, and facilitate route planning (Baumann and Mattingley 2021; Patai and Spiers 2021), our findings suggest that their structural attributes might not directly reflect wayfinding abilities. This discrepancy between structural and functional data highlights the complexity and variety of spatial navigation and associated cognitive processes. Our data align with the hypothesis that the parahippocampal area is specialized in landmark recognition, functioning similarly to face recognition (Epstein and Vass 2014). Given that landmark recognition played a very minor role in our experiment, this specialization may explain why the structural attributes of the parahippocampal region did not correlate with wayfinding performance. Regarding the entorhinal cortex, its activities might be directly linked to one of the hippocampi, as observed through functional connectivity changes for London taxi drivers compared with non-driver participants (Peng et al. 2018).

Beyond the core spatial navigation regions, our study found that the volumes of two frontal areas, part of the primary motor cortex and a cerebellar lobule, were positively correlated with wayfinding performance. Consistent with prior literature, larger volumes in the TrIFG and the right SFG would support several cognitive processes: (i) making sequential decisions during path planning, (ii) monitoring progress towards the goal by anticipating key landmarks or junctions and tracking self-motion relative to previous locations, and (iii) supporting active decision-making at junctions (Patai and Spiers 2021). These findings reinforce the general idea that wayfinding is a complex task engaging a broad network of brain areas (Baumann and Mattingley 2021).

In addition, a potential contribution from the cerebellum was investigated. Although the cerebellum is often overlooked, activations in several regions of its posterior lobe have been observed during tasks involving executive functions such as planning, organizing, and strategy formation (Schmahmann 2019). In our study, only the volume of the bilateral VIIIB lobules was found to be associated with wayfinding performance. This region has been previously linked to various tasks that engage executive functions (Schmahmann 2019; Stoodley and Schmahmann 2009), emotional processing (Stoodley et al. 2012), and mental rotation (Stoodley et al. 2012). In the specific context of our study, mental rotation abilities could help convert coordinates from the simulated world to the navigational map and vice versa. In addition, participants might envision different possible paths to reach various locations, select a travel option, and potentially change

the selected path during the trip. Therefore, cognitive processes related to visual divergent thinking could also be required (Gao et al. 2020). A complementary interpretation would be that the cerebellum is involved in the construction of cognitive maps, as the cerebellum has been reported to be involved in goal-directed navigation in mouse models (Rochefort et al. 2013). Finally, it must be noted that lobule VIIA-Crus I of the left cerebellum was found to be just above the cutoff we set for the VIP values in the PLS regression. This could be related to previous results (Iglói et al. 2015), showing that place-based spatial navigation functionally involved the right hippocampus and the left cerebellar VIIA-Crus I. The importance of Crus I in spatial navigation has also been found in structural investigation (Ramanoël et al. 2023).

Among the various factors known to influence navigation skills, gender, and driving experience emerged as significant covariates in our regression models, both being associated with wayfinding performance. The influence of gender aligns with well-established findings in the literature (Coutrot et al. 2022; Munion et al. 2019). In addition, greater self-reported driving experience correlated with better wayfinding performance, highlighting the importance of considering this variable in spatial navigation research. In contrast, age, video gaming experience, and self-reported driving frequency were not significantly associated with wayfinding performance. The lack of association with age may be due to the relative homogeneity of our sample, which consisted mostly of young adults, making it insufficient to capture age-related differences in brain structure. A similar rationale could apply to the video gaming experience, as the sample included participants with either very little or substantial gaming experience, potentially diluting the effect. As for driving frequency, it seems that frequent driving alone may not be sufficient to enhance navigation skills—what matters more may be the diversity of environments navigated. For instance, one could drive many kilometers per year within a familiar area, whereas another might drive less but frequently explore new locations, which could foster stronger navigational abilities. These interpretations should be approached with caution, as the experiment was not specifically designed to examine inter-individual differences. A more rigorous investigation of these factors would require a significantly larger and more diverse sample of participants to draw robust conclusions.

The construction of a complete and detailed cognitive map was not necessary for the wayfinding task, as participants had continuous access to a navigational map. However, they could not constantly look at the map all the time because driving required ongoing visual attention to the environment (Navarro et al. 2020, 2021). Thus, driving and navigation tasks competed for visual resources. Interestingly, top performers spent more time gazing at the map than low performers, highlighting the benefit of using external aids in wayfinding performance. There was no significant correlation between wayfinding performance and the number of visits to the map, suggesting that top performers did not consult the navigational map more often but rather look at that map for longer periods. Therefore, spending more time looking at the map was the strategy that benefited the best performers. The nature of this benefit could be related to a direct use of the information available on the map and/or to memorizing spatial information (i.e., building a cognitive map).

In either case, this supports the idea that survey mapping was still required by the wayfinding task during actual navigation (Lobben 2004). The wayfinding task was difficult enough to require participants to explore the environment based on the navigational map to achieve better performance.

To explore a significant portion of everyday spatial navigation situations, a navigational map was used in conjunction with in situ exploration (Allen 1999). Based on Wiener et al. (2009) classification, the continuous presence of the map was expected to enhance the scaled representation of the environment and the spatial relationships between locations, thereby facilitating target location and pathfinding. Within the framework of Human-Technology Symbiosis (HTS), the brain structures associated with wayfinding performances reinforce the hypothesis that such external tools do not merely assist users; they modify the wayfinding task itself, influencing and shaping cognitive processes as well as the neural bases of these processes (Navarro 2017a, 2017b; Navarro and Hancock 2023). Whether these brain structures are adaptations vestigial of unaided navigational abilities or the product of HTS remains under debate.

Numerous avenues for further exploration and enhancement are feasible. The choice not to dig into wayfinding strategies was made, but strategies could have an impact on performances (Farr et al. 2012; Hegarty et al. 2023; Spiers and Maguire 2008). Further investigations based on a larger sample of participants would allow the assessment of the strategies used by participants and see how these strategies interact with the wayfinding performances and associated cerebral structures. Increasing the sample size would also allow for a more detailed analysis of individual characteristics (Coutrot et al. 2022). The wayfinding task effectively highlighted differences among participants, with the total number of reached locations varying widely. In addition, a larger sample size would be required to confirm the findings, considering a sample of participants with more varied characteristics such as diverse nationalities, navigational habits, and driving abilities, for instance. Seventeen participants found four locations or fewer, while sixteen found five or more. Comparing these findings with data from professional drivers, who likely possess superior spatial navigation skills, could provide valuable insights into differences in brain structure volume and visual behaviors. While the reported work provides evidence of brain structure specialization to support wayfinding performance, extending the ecological validity of such evidence would be highly relevant in future investigations. Factors such as time of day, weather, and visibility can significantly impact navigation, and exploring diverse conditions like nighttime or reduced visibility would provide a more comprehensive understanding. In addition, navigation skills gained in one context, such as frequent hiking or navigating complex buildings, might transfer to road navigation and vice versa. Some wayfinding abilities may thus be domain-general, while others remain environment-specific. Investigating a wider range of environments would not only strengthen the ecological validity of these findings but also offer insight into the transferability of navigation skills across different contexts. In addition, further research is needed to explore how the use of navigational maps and modern tools like GPS alters spatial navigation tasks, associated cognitive processes, and neural foundations. It is plausible that spatial navigation abilities differ significantly between unaided and aided navigation.



## 5 | Conclusion

This study examined navigational map-based wayfinding performance in an unfamiliar virtual environment along with participants' brain structural MRI scans. The study highlights the significant roles of the volumes of the right hippocampus, left PCgG, TrIFG, right SFG, and right cerebellar lobule VIIb in supporting wayfinding performance, implying a complex network of brain areas involved in navigation. Interestingly, more gray matter density in an anterior cluster located in the right hippocampus correlated with poorer wayfinding performances, whereas most posterior gray matter density correlates with better performances. Altogether, these results underscore the specialization of brain structure in supporting spatial wayfinding tasks. This highlights the intricate relationship between specific brain regions and their roles in navigation, emphasizing how structural adaptations contribute to spatial navigation performance. These findings pave the way for deeper investigations into the neural mechanisms underlying wayfinding and the potential impacts of navigational aids on cognitive and neural processes.

### Author Contributions

J.N. and E.R. conceived and designed the study. M.C.O. provided the driving simulation software. J.N., D.S., P.S., and E.R. performed the experiments and collected the data. Data analysis and interpretation were conducted by J.N., D.S., J.R., and E.R. The manuscript was drafted by J.N. and revised critically for important intellectual content by E.R. All authors approved the final version of the manuscript for submission.

### Acknowledgments

This work was performed within the framework of the project AUTODRIVE (ANR-18-CE22-0002-01). The authors are grateful to Emma Hernout and Dorine Henry for their contribution to the design of the simulated environment. The authors used Chat GPT 3.5 for English proofreading purposes exclusively.

### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The data that support the findings of this study are available from the corresponding author, JN, upon reasonable request.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section.