The effect of virtual reality modality level of immersion and locomotion on spatial learning and gaze measures

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Abstract

The widespread adoption of head-mounted display (HMD) virtual reality (VR) systems has emerged in various fields, including spatial learning research. This study investigated the effects of VR modality level of immersion, locomotion interface, and proprioception on spatial learning and physiological measures using eye-tracking (ET) in VR. We translated the classic T-maze task from Barnes et al. (1980) to humans for the first time, comparing three VR modalities: 3D HMD VR with physical walking, 3D HMD VR with controller-based movement, and 2D desktop VR. Results revealed that human participants employed a mixture of cue, place, and response strategies when navigating the virtual T-maze, mirroring rodent behavior. In both samples, no significant differences were found between the two HMD VR conditions in learning performance, nor consistent ones in strategy choices. However, 2D desktop navigation was associated with slower initial learning, though this discrepancy diminished in subsequent sessions. These results were supported by spatial presence, immersion, and naturalness reports. Gaze measures showed that participants who physically walked devoted more visual attention to environmental cues compared to controller users. Predictive models for identifying spatial learning strategies based on ET and behavioral measures demonstrated significant accuracy in some models, particularly in the VR walking condition and second session. Our findings enhance the understanding of spatial learning strategies and the effects of VR modality on cognition and gaze behavior. This work demonstrates the potential of integrated ET data and holds implications for early detection and personalized rehabilitation of neurodegenerative conditions related to spatial cognition.

Keywords:
Spatial learning; Strategy; Virtual reality; Immersion; Proprioception; Gaze behavior; Eye-tracking;

1 Introduction

1.1 Spatial learning strategies

Spatial navigation is a multifaceted cognitive process involving diverse strategies that allow individuals across all species to orient themselves and locate goals in their environment. Two core spatial learning strategies, place, and response, have been the focus of research since Tolman's seminal work (Tolman et al. 1946). In that study, Tolman et al. constructed a cross-maze paradigm (a T-maze with two possible opposite starting points, one in training and the other in the test phase) and demonstrated that rodents could navigate using a place strategy, that relies on forming a cognitive map based on environmental spatial cues, or a response strategy, that depends on fixed motor patterns such as always turning left or right. These findings introduced the concept of flexible navigation, challenging behaviorist paradigms that emphasized stimulus-response (S-R) associations (Goodman 2021).

These strategies are also frequently referred to as allocentric and egocentric navigation. Allocentric navigation (place strategy) involves creating a representation of the environment from an external perspective, anchored to spatial landmarks or geometric relationships independent of the individual's position (O'Keefe and Nadel 1978). In contrast, egocentric navigation (response strategy) relies on a self-centered perspective, encoding routes or turns relative to the individual's body axis. These complementary systems enable flexible and habitual navigation and are crucial for adapting to dynamic environments (Iaria et al. 2003).

Building on Tolman's foundation, another study (Barnes et al. 1980) expanded the T-maze paradigm to include a third strategy in addition to place and response, the cue (beacon) strategy, where animals navigate toward a distinct intra-maze landmark, which was a rubber mat in their design. Their experimental design included three types of probe trials, in which each strategy was tested by rotating the starting point in 180^0, rotating the outer-maze objects in 180^0, or shifting the intra-maze cue (see illustration in Fig. 1). This innovative study allowed the dissociation of three navigation strategies and

the examination of age-related preferences. Older rodents were shown to favor simpler response strategies over hippocampal-dependent place strategies, highlighting the dynamic interaction between these systems.

In addition to the T-maze, other paradigms provided additional insights into the place and response spatial learning strategies, where the Morris Water Maze (MWM) (Morris 1981) and the Radial Arm Maze (RAM) (Olton and Samuelson 1976) tasks are most widely used. The RAM consists of multiple arms (8 in the initial version) radiating from a central hub, some of which contain food rewards (Olton and Samuelson 1976). It tests working memory (avoiding re-entry to previously visited arms) and reference memory (learning which arms consistently contain rewards). In the MWM (Morris 1981), rodents were trained to locate a hidden platform submerged in a circular pool of opaque water. In the original version of the MWM, rats were required to use distal environmental cues for navigation (place-based). Variations of the task allowed animals to use cue (beacon) strategy and also test for using response strategy when altering the starting point (Morris 1984).

1.2 Translation to humans

Due to the wealth of knowledge derived from animal studies, translating these paradigms to humans has been a significant area of research in cognitive neuroscience. To name a few, the version of the two possible strategies of the T-maze (Levy et al. 2005; Astur et al. 2016; Lin et al. 2022; Gammeri et al. 2022), RAM (Moffat et al. 1998; Iaria et al. 2003; Astur et al. 2004, 2016; Bohbot et al. 2007; Etchamendy et al. 2012; Konishi et al. 2013; Mennenga et al. 2014; Robaey et al. 2016; Kim et al. 2018; Ben-Zeev et al. 2020; Palombi et al. 2022), and MWM (Astur et al. 2004; Levy et al. 2005; Schoenfeld et al. 2017; Ben-Zeev et al. 2020), and even some of their combinations (Astur et al. 2004; Levy et al. 2005; Ben-Zeev et al. 2020) have all been adapted for human studies, with varying degrees of immersion and technological implementation. These tasks focused either on memory (RAM), or one or two possible strategies of place, and response or cue (T-maze, MWM). Some consider the T-maze as the best paradigm to evaluate learning behavior in mice and the simplest way to assess spatial learning strategies (Sharma et al. 2010). However, to the best of our knowledge (Moffat 2009), there are no published studies yet that explore the cue strategy introduced by (Barnes et al. 1980) in addition to place and response, in the T- maze task in humans.

The particular use of one of three spatial learning strategies of place, response, and cue (beacon) was studied in humans in a 2D virtual plus maze (de Condappa and Wiener 2016) and compared between young and old age groups (Wiener et al. 2013). In this paradigm, each plus junction included two landmarks, one on each side. The associative cue strategy involved learning a specific directional response at a landmark, while the beacon strategy entailed moving towards a landmark associated with the goal (the learned turn), and the allocentric strategy involved the creation of a cognitive map of the configuration of the landmarks, which was the only one similar to (Barnes et al. 1980). There are a few key differences between the plus maze and the T-maze paradigms, even though they both examine three strategies. The test trials in the plus maze were approached from different angles, and only using the place strategy led to the correct choice, while in the T-maze, all test trials were approached from the same angle as in training, and the maze setup was altered such that there was no right or wrong choice. In addition, the egocentric strategies in the plus maze were defined by the same landmarks that defined the place strategy which may lead to some ambiguity of the strategies especially in the 180^0 angle, when it seems that place and beacon strategies may concur, whereas in the T-maze, all the strategies were completely independent of each other. Another study investigated navigating these three strategies in a virtual sunburst maze, which was a replica of Tolman's classic rodent study (Doner et al. 2023). In the test phase, the original fixed path was blocked, and participants faced 18 radiating hallways (a "sunburst" configuration) to choose an alternative route. It was found that when participants were required to take a shortcut (direct paths to the goal), they consistently employed non-optimal response strategies either following the encoded route or using light as a beacon cue, even when distal boundary cues or enhanced idiothetic cues were added, both in the 2D desktop and the head-mounted displayed virtual reality (HMD VR) versions. In this study as well, there was an optimal route in the test phase that was based on allocentric strategy, differently than in the T-maze.

1.3 Spatial learning in VR

Naturally, the first translations of the spatial learning tasks to humans used a 2D screen display of a virtual environment (VE), and as in other fields of research, in the last decade, the 3D HMD VR has also spread to spatial learning. This approach offers several advantages over traditional 2D or non-immersive paradigms. First, HMD VR provides a more ecologically valid environment for assessing navigation abilities (Vigliocco et al. 2024). For example, the effects of mild aerobic exercise on spatial learning performance in both MWM and RAM were investigated in an HMD VR while navigating with the controller following head movements (Ben-Zeev et al. 2020). In addition, HMD VR allows for full-body movement, as was recently studied in a physically walkable T-maze (Lin et al. 2022). Eventually, it increases the

sense of presence that closely mimics real-world navigation (Huffman and Ekstrom 2019). This increased validity may lead to more accurate assessments of spatial cognition and strategy use.

Together with the advantages of advancing from 2D research setups to immersive 3D HMD environments in spatial learning, it is essential to compare these modalities to understand how differences in interaction and immersion affect spatial learning outcomes. Such comparisons are critical for accurately interpreting results across platforms (Huffman and Ekstrom 2019) and for ensuring that findings from 3D HMD studies are grounded in the extensive body of work developed in 2D environments over decays (Hejtmanek et al. 2020). This approach mirrors the importance of bridging findings and paradigms between animal and human research, allowing for deeper insights into spatial cognition across contexts and species (Schoenfeld et al. 2017).

Efforts to investigate how VR modalities influence navigation-related cognitive processes have led to direct comparisons between real-world and VR environments, as well as between different VR systems and interfaces. For instance, the navigation performance in real-world environments was compared to HMD VR setups (Martelli et al. 2019), revealing differences in the use of spatial cues and exit times between these conditions. This study demonstrated that immersive VR could effectively replicate some aspects of real-world navigation while highlighting the impact of visual and environmental fidelity on spatial learning. Similarly, differences in navigation and learning across VR systems with varying levels of immersion were explored (Hejtmanek et al. 2020), including real-world learning, HMD VR with an omnidirectional treadmill, and desktop VR using a mouse and keyboard. They found that physically engaging systems, such as real-world and treadmill-based VR, enhanced spatial memory and cognitive map accuracy compared to static desktop VR. In addition, HMD VR and desktop versions of an 8-arm RAM were compared (Kim et al. 2018), measuring working memory errors, reference memory errors, and other behavioral metrics. The study found that while performance did not significantly differ between the two modalities, HMD VR elicited greater subjective presence and immersion, emphasizing the potential advantages of immersive systems for engaging participants in spatial tasks. Additionally, fully virtual environments reconstructed from real-world spaces were compared to augmented reality (AR) in real-world settings (Mayrose and Maidenbaum 2024), and no significant differences were found in subjective reports as immersion or objective spatial memory performance, suggesting that AR and VR may be used interchangeably in some contexts.

When the role of proprioception, body-based information of movement and rotation, on spatial learning was studied (Ruddle et al. 2011), it was found that proprioceptive feedback significantly improved the accuracy of cognitive maps in VR environments. Notwithstanding, another study suggested that the neural correlates of spatial retrieval tasks with functional magnetic resonance
imaging (fMRI) are modality-independent based on the three VR levels of body-based and joystick movement tested (Huffman and Ekstrom 2019). The impact of locomotion interfaces in HMD VR was further examined by comparing controller-based navigation interfaces and assessing their influence on performance and subjective experiences such as presence and immersion (Lim et al. 2022). This study highlighted how interface design could modulate cognitive load and navigation efficiency, with more intuitive interfaces generally yielding better outcomes.

These studies demonstrate substantial research exploring the effects of VR modality and locomotion interfaces on spatial learning, focusing on metrics such as accuracy, immersion, memory, and neural correlates. However, no studies to date have directly tested the influence of VR modality and locomotion interface on spatial learning strategies of cue, place, and response. While strategy usage across two desktop VR samples and one HMD VR sample was recently examined (Doner et al. 2023), the HMD VR sample was significantly smaller than the 2D, and the participants completed all conditions sequentially, unlike the 2D samples, where participants were assigned to a single condition. These studies collectively underscore the need to systematically compare 2D and various 3D VR modalities, levels of immersion as well as different locomotion interfaces, to fully understand their effects on spatial learning, and highlight the need for more controlled comparisons to isolate the effects of VR modality on strategy selection.

1.4 Physiological representation of spatial learning

Visual information processing plays a critical role in how we represent and navigate space (Ekstrom 2015), pointing at eye-tracking (ET) as a valuable method for investigating cognitive processes during spatial navigation tasks. ET offers a unique, real-time window into the visual and cognitive processes guiding navigation and has been shown to reveal subtle differences in strategy usage. One study, (Livingstone-Lee et al. 2011) demonstrated that gaze behavior within the first second of a navigation trial could differentiate between allocentric and egocentric strategies in a VR Morris Water Maze (MWM). Another study, (de Condappa and Wiener 2016) examined gaze and pupillometry data to identify navigation strategies in a plus maze, finding that gaze behavior reflected the movement direction during learning and decision-making which was unrelated to the used strategy. They additionally observed that increases in pupil dilation indicated a shift to a more cognitively demanding place strategy. Similarly, gaze dynamics in naturalistic settings have revealed cue preferences (e.g., landmarks versus geometry) that correspond to specific navigation strategies (Bécu et al.

2020), pointing to the utility of visual data for understanding navigation mechanisms. These studies demonstrate the variability in gaze behavior and its relation to strategy across studies, stressing the need for further assessment of this relation.

The integration of ET with VR technology has opened new avenues for spatial navigation research. The viewing behavior during VR navigation was studied using a graph-theoretical analysis approach, revealing complex patterns of visual attention allocation in urban environments (Walter et al. 2022). In addition, another study (Zhu et al. 2022) demonstrated that gaze patterns dynamically adapted to environmental complexity and task demands, balancing attention between environmental transitions and hidden goals during spatial planning in controller-base movement. Likewise, another study (Drewes et al. 2021) compared gaze behavior in VR with controller-based movement to real-world locomotion, highlighting both similarities and differences in visual exploration strategies.

One significant advantage of modern VR headsets is the integration of ET capabilities directly into the device. This built-in functionality eliminates the need for additional equipment, simplifying data collection and improving ecological validity. For example, (Hougaard et al. 2021) utilized the ET capabilities of an HTC Vive headset to study gaze patterns in a virtual museum environment, demonstrating the feasibility of such integrated systems for spatial cognition research.

While ET provides valuable insights, other physiological signals have also been explored in VR spatial navigation studies. A previous study (Lin et al. 2022) combined a physically walkable T-maze with random reward location in VR with EEG recordings and found neural correlates of navigation decisions. Another study, (Do et al. 2021) recorded EEG signals during VR navigation with physical walking, providing insights into brain dynamics during active spatial exploration related to head direction. These studies highlight the potential of combining multiple physiological measures with VR to gain a more comprehensive understanding of spatial cognition. Nevertheless, ET offers unique advantages as a physiological measure in VR navigation studies. Unlike EEG or other techniques requiring additional equipment, ET is seamlessly integrated into many VR headsets, minimizing participant discomfort and maintaining a high degree of ecological validity.

1.5 Current research

Considering the growing interest in revealing the effect VR modalities have on cognitive processes, this work aimed to assess how the VR modality level of immersion and locomotion interface affect spatial learning measures, particularly the utilization of spatial learning strategies. For this purpose, we translated for the first time the classic T-maze task form (Barnes et al. 1980) to humans. Therefore, we also aimed to find out whether this elegant task allows the disentanglement of three spatial learning strategies of cue, place, and response for humans as in rodents. We compared three conditions to explore how VR modality and locomotion interfaces influence learning measures in this task. In two of them, the environment was displayed on a 3D HMD VR while physically walking in the first and standing in place and using the controller in the second, and in the third, the environment was displayed on a regular 2D screen using the mouse and keyboard for navigation. In addition, we collected spatial presence and awareness questionnaires, as well as widely used spatial abilities tests to test for their relation to strategies usage.

In addition, in the two HMD VR conditions, we aimed to leverage the advantage of the headset's built-in ET device, by analyzing ET data collected during our translation of the T-maze task for a two pronged-approach. First, we aimed to examine how VR modality and locomotion methods affect gaze behavior. By comparing ET data across different VR conditions (walking vs. controller-based movement), we aimed to study how the level of immersion and physical engagement influence visual exploration and strategy selection in spatial navigation. Second, we aimed to identify the different spatial learning strategies based on physiological (i.e. ET) data. We tested whether gaze features will differentiate strategy selection as in (Livingstone-Lee et al. 2011) where gaze distinguished allocentric and egocentric navigation, or display mixed association to strategies as in (de Condappa and Wiener 2016) where gaze behavior was unrelated to the used strategy. To achieve this, we developed predictive models to infer navigation strategies from these data alone. Such models could have significant implications for understanding individual differences in spatial cognition and potentially aid in the early detection and rehabilitation of navigation impairments associated with various neurological conditions such as Parkinson's disease (PD) (Schneider et al. 2017) and Alzheimer's disease (AD) (Lithfous et al. 2013).

Interestingly, among the spatial navigation tasks studied in humans, the T-maze seems to fairly mimic navigation tasks humans still encounter in places where digital navigation assistance is not applicable. For example, finding your car in a big parking lot, the info desk in a museum, or the electronics service desk in a huge shopping mall. Thereby, this work aims to fill a gap in the translational research literature and provide a deeper understanding of human spatial navigation in daily life and its associated gaze behavior, in addition to the VR modality's effect on it, which holds implications for both healthy and clinical populations.

2 Methods

2.1 Code and data availability

All the data and the codes for data handling, pre-processing, analysis, and Unity task projects are available in the Open Science Framework (OSF, project page: Peer_review_link).

2.2 Preregistration

Following data collection on the first sample, we pre-registered the behavioral results and the required sample size for their replication with 80% power (see the preregistration section in the OSF project). All analyses that were added following the second sample's data collection and exploration were mentioned explicitly in the text. The ET analyses were performed following data collection of the two samples. We analyzed the first sample's results and preregistered the models and hypotheses based on these results prior to observing the second sample's data. Briefly, all the significant effects that were obtained on the first sample were preregistered, and those that were obtained only on the second sample were not.

2.3. Participants

The participants recruited for this study were healthy, with intact or corrected vision, and aged 18 - 40. The pre-defined experiment exclusion criteria were: participants with dizziness, pregnant women, and participants with eyeglasses only for near vision correction (not contact lenses; according to eye-tracker manufacture instructions). Participants gave their informed consent to participate in the experiment and received monetary compensation for their time of ~ 12$ per hour. The study was approved by the institutional ethics committee.

This study was performed on two samples. We aimed to obtain 48 valid participants, for the first sample, 16 in each of the three experimental conditions. The virtual environment consisted of 8 design options that accounted for 2^3 setup variations. This resulted in a target of two participants in each setup option and each experimental condition. For this purpose, we recruited a sample of 53 participants. Two participants did not complete the task due to their difficulty using the mouse and keyboard to navigate the environment, which led to the incompletion of the experiment at its allotted time. Participants were considered valid if the data for the two task sessions were collected and saved properly. Five participants had only one valid session due to software failure and shut down in the middle of the session. Therefore, these participants were excluded from further analysis. This conlcluded the first sample with 46 valid participants (mean age: 26.4, SD:5.3, 27 females).

We performed power analysis on the behavioral results of this sample and calculated the minimal sample size required to obtain 80% power with p-value < = 0.05 for the effects that were obtained on the first sample. Power analysis resulted in a target sample of 75 valid participants, 25 in each experimental condition, which was noted in the preregistration. A total of 88 participants were recruited to obtain an n=75 of valid participants (mean age: 27.48, SD:5.3, 49 females). Thirteen participants were excluded due to the following reasons: one participant stopped the experiment due to their report of dizziness; two participants did not learn to navigate the environment in the experiment's allotted time (one in the 2D condition and one using the controller); and ten participants had only one valid session due to software failure or shut down in the middle of the session. The demographic details of the two samples are shown in Table 1.

Table 1. Participants' demographic data.

S (N)	Condition	Age mean (SD)	Frequency of playing computer games mean (SD)	VR experience N (%)	Females N (%)
1 (46)	2D	25.6 (5.2)	2.1 (1)	11 (73)	6 (40)
	Controller	26.3 (5.4)	1.6 (0.9)	12 (80)	11 (73)
	Walk	27.5 (5.3)	1.75 (1.1)	9 (56)	10 (67)
2 (75)	2D	27 (4.5)	1.96 (1.4)	17 (68)	13 (52)
	Controller	26.9 (5.9)	1.92 (1)	15 (60)	18 (72)
	Walk	28.5 (5.1)	1.76 (1.3)	21 (84)	18 (72)

Note: The participants' demographic data is presented according to sample (noted as S) and experimental condition. The frequency of playing computer games was selected on a 5-point scale from 1 (not at all) to 5 (every day). SD stands for standard deviation (see section *3.7 Demographic data* in the *Results* for the corresponding statistical analysis).

2.4 Experimental setup

All the virtual environments were executed on a computer equipped with an i9-10900f CPU running at 2.80 GHz, 64 GB of RAM, an NVIDIA GeForce RTX 2080 super GPU, and a 64-bit Windows 10 operating system. The virtual environment and task code were developed in C# in Unity 3D (version 2019.4). The 2D virtual environment was displayed on a screen with a 1920× 1080 resolution and a 60 Hz refresh rate.

The 3D VR conditions (the walking and using the controller conditions) were performed using a wireless VR headset adapted with a built-in binocular eye-tracking (ET) device (HTC VIVE Pro Eye). The eye-tracker (manufactured by Tobii®) provided data on eye openness, pupil diameter, eye gaze, and head movement during participants' engagement in the VR task. The manufacture ET accuracy was $0.5\text{-}1.1^0$ and the sampling frequency was 120 Hz. However, the samples were collected at ~90 Hz de facto, probably due to using the wireless adaptor rather than a direct connection to the computer. The VIVE Pro Eye displayed a resolution of 1440 x 1600 pixels per eye, with a trackable field of view of 110 degrees and a 90 Hz refresh rate. The acquisition of ET data was seamlessly integrated into the task through the HTC SRanipal software development kit (SDK) for Unity, which was customized to meet the task's design and specifications.

The VR task and scene were designed according to the design of Barnes et al. (Barnes et al. 1980). The objects were uniquely modeled in Blender and imported to Unity. The participants controlled navigating the embedded task instructions using a trigger press on the controller in the VR conditions or the escape key in the 2D condition.

2.5 Experimental procedure

With the purpose of studying individual differences in spatial learning strategies, we translated the classical spatial learning 3-arm T-maze task (Barnes et al. 1980) for the first time to humans in VR.

2.5.1 General Design

The maze was centered in the middle of the VR arena and was surrounded by five external cues (two of them are presented in the scheme in Fig. 1). In addition to these cues, one of the arms was textured with brick texture, differently than the others, according to task conditions as was the cued arm in the original task. The illustration of the environment shown in Fig. 1 is characterized by a right-cued arm. The task consisted of navigating to one of two arms in each trial to find the reward (in Fig. 1 it is positioned at the right arm).

2.5.2 Behavioral Task

The task started with training trials by placing the participant at the beginning of the start arm. Each trial finished when the participant reached the end of one of the two T arms to find the reward which was a golden coin (Fig. 2). When participants reached the end of the rewarded arm, a golden coin appeared in front of them (in the right arm in the illustration in Fig .1), and upon their collection of it the message "+1 coin added" appeared in front of them. When participants reached the end of the unrewarded arm the message "+0 coin added" appeared in front of them. We added a return path to the beginning of the start arm between each two consecutive trials. As in the original article (Barnes et al. 1980) once four consecutive success trials were achieved the probe phase began.

Following the training phase, three types of test probe trials were performed, during which a turn to one of the maze arms represented an explicit choice in the strategy tested over the two others. Each strategy testing probe trial was preceded and followed by a regular probe trial identical to a training trial (see Fig .1). Therefore, the test probe trials were given as a series of six trials, where trials 1, 3, and 5 were regular trials (set up as in the training phase) and trials 2, 4, and 6 were each of the three test probe trials that were organized in a random order (an example for such a setting is shown in Fig. 1). Three consequent probe series were performed, which generated three test probe trials for each strategy.

To avoid new learning of the probe setups or extinction of the training, during the probe trials, both goal arms contained a masked silver coin, and upon the participants' collecting it, the message "? coin added" appeared in front of them. Before they began the task, the participants were informed that the value of a silver coin could either be equivalent to that of a gold coin or have no value at all. The participants were instructed to find as many gold coins and silver coins with gold coin value as possible and were incentivized to receive an additional monetary bonus proportional to the number of these collected coins (without their knowing that all of them received the same bonus of ~2.6$ at the end). We explained to the participants that these are two distinguished parts of the task and that from the moment they would first find a masked silver coin, they would always find masked silver coins.

Fig. 1: Task design. The test probe trials include cue (2), place (4), and response (6), and the regular probe trials (1,3 and 5) are identical to training.

Cue probe: The textured arm interchanged with the other (Fig. 1 (2)). When referring to the example presented in Fig. 1, in case the participant continued to turn to the cued arm they used a different turning response (left instead of right) and ended in a different place. Thus, by elimination, they used the 'cue' strategy.

Place probe: The entire maze was rotated by 180^0 (Fig. 1 (4)). This implies that, for the example presented in Fig. 1, if the participant turned to the same spatial place, they used a different response and went to an arm with a different cue. This implies that they used a 'place' strategy.

Response probe: The start arm was rotated by 180^0 (Fig. 1 (6)). For the example presented in Fig. 1, if the participant used the same turning response (right) they went to an arm with a different cue and ended in a different place. Hence, this participant used a 'response' strategy.

The participants were assigned to one of the 8 counterbalanced conditions that determined the maze setup: whether the textured arm (cue) was the rewarded arm, the position of the goal arm to the left or the right of the start arm (response), and the location of the start arm in relation to the spatial cues (place).

Fig. 2: The T-maze setup. **a:** The view when entering the center of the T-maze from the start arm. **b:** A representation of a participant's hand reaching to collect the found coin.

Each participant performed two sessions that included training trials and the subsequent probe trials for two complementary maze setups, such that no matter which strategy was used, new learning was required to find the reward during the second session.

We compared three levels of immersion and locomotion (Fig. 3): 1) participants wore a 3D HMD VR headset and physically walked in the arena (Fig. 3A); 2) participants wore a 3D HMD VR headset and used the VIVE controller for movement while they were physically standing in place (Fig. 3B); and 3) participants set in front of a 2D regular screen display and used the mouse and keyboard for movement (Fig. 3C). In all experimental setups, virtual avatar of the participant's dominant hand appeared in front of them and changed position and perspective according to their movement in the scene. In the VR conditions, the participants reached out their dominant hand that held the controller to collect the coin when they approached it. In the 2D condition, the participants moved towards the coin using the mouse and keyboard until it collided with the coin and picked it up as a result.

Fig. 3: Experimental groups. **a:** 3D HMD with actual walking. **b:** 3D HMD standing and walking with a controller. **c:** 2D screen display using a mouse and a keyboard for movement.

2.6 Raw data

The data was logged with a time stamp readout in microseconds precision that allowed synchronization of the data with the task events timeline. In all the experimental conditions, the 3D (x,y,z) position and rotation of the participants were recorded. In the 3D HMD conditions additional ET measurements were gathered with the SRanipal SDK including 3D (x,y,z) gazed ray origin and direction, pupil diameter (mm), eye-openness (EO), and sample validity defined by the eye-tracker. We added the collection of the following variables: the gazed object name; the 3D (x,y,z) gazed object position, for which we considered the center of the object's bounding box; and the 3D (x,y,z) gazed ray hit point, which was the location of collision of the gaze ray with the gazed object. Samples validity and time stamps were used for trial validity analysis as detailed in the *Eye-tracking data pre-processing* section below.

2.7 Data handling

Data extraction, parsing, arrangement, fusion, and processing were performed with Python 3.12.3 (https://www.python.org/).

2.8 Eye-tracking data pre-processing

ET samples with EO ≤ 0.5 were considered as blinks. Nan values or non-valid samples, as defined by SRanipal SDK, were also treated as blinks. Samples in a time window of 150 ms before and after each blink were scrubbed, as done previously (Salomon et al. 2019).

2.9 Extracted measures

2.9.1 Learning measures

We defined the participants' learning pace as the number of training trials to reach the learning criterion (the minimum was 4 trials). Learning effectiveness was considered as the number of successful probe trials that were identical to training trials (out of a total of 9 trials). Eventually, for each of the three strategies test probe trials, we examined the explicit choices in the tested strategy.

2.9.2 Path measures

For all VR modalities, we extracted 10 descriptive path measures. We examined the path length and average speed from several perspectives: the entire trial, from the start position to the center of the maze (the section from point S to point C in Fig.4), from the center to the start of one of the maze's arms (the section from point C to point A in Fig. 4), and from the beginning of the maze arm to its end (the section from point A to point E in Fig. 4). In addition, we calculated the number of visits to the maze's center (point C in Fig. 4), and the number of enters to arms (visits in point A in Fig. 4) as measures of exploration or uncertainty in the trial, where the minimum per trial for both is one.

Fig. 4: Physiological and behavioral data in the maze. Scatter plot of a participant's data in one training trial. The participant's position in the scene (filled rectangle) and their gaze hit point position (plus marker) are displayed on top of the top view of the maze scenery in the arena. The dimensions in the scheme represent the rendered physical dimensions in the virtual environment which are in 1:1 ratio to the real-world scale in meters. The data are color-coded by the time relative to the beginning of the trial, with blue to cyan colormap for the participant's position and red to green colormap for gaze hit points position. Five colored circles with the notion O1 - O5 represent the position of the center of the maze's five surrounding objects. The colored plus markers surrounding the centers of these objects represent the gaze hit points while looking at them and are positioned on their corresponding collider object. The points marked by a white circle with a black cross in the middle denote physical locations of interest in the maze, which are relevant to the path analysis. The starting point is denoted by S, the center of the maze by C, the beginning of one arm by A (the left one with respect to the participant is shown as an example), and the end of that arm by E (the left one with respect to the participant is shown as an example).

2.9.3 Eye-tracking measures

We extracted ET features to engulf the gaze behavior in every trial based on (Gabay and Schonberg 2023). For each trial, we extracted global features that comprised of 6 pupil features, 3 per eye, pupil diameter (10th, 50th, 95th percentiles); and 5 blinks features including number of blinks, total blinks duration, minimum, maximum, and mean of blinks length based on constraints (Pietrock et al. 2019). In addition, we extracted object-related features that consisted of: 1 feature of percent-time the object was gazed at out of the entire trial duration;12 dispersion patterns of gaze hit points features which comprised of the (10, 50, 95) percentiles of the Euclidian distance between the gazed hit point to the centroid

of the gazed object that we named as gaze shift distance; these distances normalized by the Euclidian distance between the gazed ray origin and the gazed object centroid; the difference in time of the gaze shift distance, and the Euclidian distance between the participant's head position and the gazed object position; and 3 gaze speed features defined as the (10, 50, 95) percentiles of the gaze scan Euclidian distance per time unit. The object-related features were computed to assess gaze behavior while looking at a single object or at a cluster of objects with a common trait of interest during the trial. An example of gaze behavior in a trial is shown in Fig. 4.

2.10 Questionnaires and tests

Following the completion of the two task sessions, the participants filled out several questionnaires on a 2D screen display. We first collected their demographic data (see details in Table 1) and continued with other thematic questionnaires and tests that were performed in the order they are mentioned in this section. The questionnaires were presented on a Google form unless mentioned otherwise.

2.10.1 Presence questionnaire

The sense of spatial presence was collected using a Hebrew translation of the ITC SOPI (Independent Television Commission Sense of Presence Inventory) presence questionnaire (Lessiter et al. 2001). This questionnaire consists of 38 statements for which the participants were asked to indicate the level of their agreement using a 5-point scale from 1 (strongly disagree) to 5 (strongly agree). The results were combined into 4-factor scores: Spatial presence, Engagement, Ecological Validity/ Naturalness, and Negative Effects. Each factor is the mean value of all the items defined as contributing to the factor.

2.10.2 Awareness questionnaire

The participants were asked for their awareness of the information each of the three strategies held in the task in a three-choice question consisting of: "yes", "in some of the trials", and "no". For example, to test their awareness level of the cue, they were asked- "have you noticed a brick texture in one of the arms?". The responses were transformed into a 3-level ordinal scale from 1 ("no") to 3 ("yes") and were used for analysis.

In addition, the participants were asked for their perception of to what degree they used each of the three strategies information on a five choice-scale of: "yes, in all trials", "in most trials", "in half of the trials", "in less than half of the trials", and "not at all, it seemed to me as a decoration". For example, to test their perception of the level of using the cue strategy, they were asked- "have you used the arms' texture (with/without bricks) to collect as many golden coins as possible?". The responses were transformed into a 5-level ordinal scale from 1 ("not at all, it seemed to me as a decoration") to 5 ("yes, in all trials") and were used for analysis.

2.10.3 Spatial abilities tests

Mental Rotations Test (MRT): The MRT requires participants to identify two out of four rotated 3D objects that are identical to a reference figure (Vandenberg and Kuse 1978) later redesigned by (Peters et al. 1995). This task assesses spatial ability by challenging participants to mentally manipulate and compare the orientations of complex shapes within a time limit. We used a Hebrew version of the validated revised version of a standard set MRT-A test that was translated and used in (Lander et al. 2020). The MRT-A version included 24 sets of images where a point was given only when the two matching figures were identified. Therefore, the test score range was 0 to 24. Following the instructions, the participants practiced four sets, and then they were given three minutes for the first two pages, and after a short break, additional three minutes for the next two pages.

Spatial Orientation Test (SOT): To examine spatial orientation ability we used a perspective-taking task that requires imagining how a scene looks from different angles (Hegarty and Waller 2004; Friedman et al. 2020). The participants were shown a spatial layout of objects and asked to imagine themselves at a specified location of one of the objects within the layout while facing another object. Then they indicated the relative direction of a target object from this imagined perspective, assessing their ability to mentally shift viewpoints. Given that the paper-based and the computer-based versions of the SOT produced similar performance (Friedman et al. 2020), we translated the computerized version to Hebrew with Python (task code available at: https://github.com/Yehuda-Bergstein/ptsot). After receiving the instructions, the participants practiced marking the answer with the mouse and were then given three examples with feedback. Lastly, the test included 12 trials with a time limit of 5 minutes. For each trial, the angular error was calculated as the deviation in degrees between the participant's response and the correct direction, with smaller errors indicating better spatial orientation ability. Performance was scored as the mean angular error of all 12 test trials.

2.11 Statistical analysis

Statistical analysis and figures were coded with R version 4.3.1. Mixed linear and mixed generalized linear models were formulated with lme4 (Bates et al. 2015) and contrast analysis with emmeans (Lenth 2024) packages. We used ggplot2 (Wickham 2016) for visualizations. The standard p-value of 0.05 was considered for assessing the significance of each effect. Bayes Factor analysis was formulated with BayesFactor (Morey and Rouder 2012), brms (Bürkner 2017), and bridgesampling (Gronau et al. 2020) packages.

2.11.1 Learning measures

We analyzed the learning pace and learning effectiveness using mixed linear models with experimental condition and session number as fixed effects and participants were considered as random effects. Since Shapiro–Wilk test showed that some of the data were not normally distributed, the models were performed on the rank of the learning measures. For each of the three strategy test probe trials, we analyzed the probability for an explicit choice in strategy using a generalized linear mixed model (GLMM) with a binomial distribution. The models' default was the VR walking condition and the first session.

2.11.2 ET measures

To test whether the level of immersion and locomotion affected gaze behavior, we examined general ET features and compared the two VR conditions. We analyzed ET measures obtained on all trials using mixed linear models with experimental condition and session number as fixed effects and participants were considered a random effect. The models' default was the VR walking condition.

2.11.3 Presence factors

The effect of the level of immersion on the sense of presence was examined using linear models, where each of the 4 presence factors was a dependent variable and the experimental condition was a categorical fixed effect. Since these factors were of ordinal scale, the models were performed on the rank of the presence factors. The models' default was the VR walking condition.

2.11.4 Awareness measures

We examined the relation between the choice of strategy to the awareness level of the information in the scene each strategy holds, the perception of using it, and whether they were affected by the VR modality. For this purpose, we used linear models, where the dependent variable was the average number of choices in strategy across the two sessions for each strategy test probe trial, and the awareness of the strategy, the perception of its usage, and the experimental condition were considered as independent variables (including interaction with the condition). Since these variables were of ordinal scale, the models were performed on the ranks of the variables. The models' default was the VR walking condition.

2.11.5 Spatial abilities measures

The spatial abilities tests were collected only from the second sample. Therefore, we did not preregister their analysis. We tested the correlation between spatial abilities and the tendency to use each strategy with linear models. In each model, the dependent variable was the mean across sessions of the number of explicit choices in the tested strategy, and the VR modality and each of the test scores of the MRT and SOT were the independent variables including their interaction. Since the dependent variables were of ordinal scale, the models were performed on the ranks of the variables. The models' default was the VR walking condition.

2.11.6 Demographic data

The differences between the two samples' demographic data were not preregistered. We added them following the second sample's data analysis. Some inconclusive findings between the two samples drove us to test for differences in the demographic data, as they might contribute to them. Each demographic variable was examined by a linear model with sample number and condition as independent variables (including their interaction).

2.12 Bayes factor analysis

All Bayes factor analyses were not preregistered. We used them as supportive analyses in cases where the results were inconclusive among the two samples, and where significant results were obtained only in one of them. These analyses were added only to the models with results that were not replicated in the second sample or found in the second sample and not in the first.

Significant effects were further assessed with BF10, which is the ratio of evidence in favor of the alternative hypothesis (H1) over the null hypothesis (H0). On the other hand, in cases where no significant effects were obtained, we computed BF01, which is the ratio of evidence in favor of the null hypothesis (H0) over the alternative hypothesis (H1). For each analysis, the alternative hypothesis was formulated by the full model with all the fixed effects, intercept, and random effects. The null hypothesis was represented by the same model as the full model, without the fixed effect of interest.

To quantify the strength of evidence for one hypothesis over another we considered the widely used frameworks (Kass and Raftery 1995; Jeffreys 1998) that provide specific thresholds guiding interpretation. Values between 1 and 3 indicated anecdotal evidence, reflecting weak support; values from 3 to 10 suggested moderate evidence, providing substantial support for one hypothesis; values from 10 to 30 represented strong evidence; values between 30 and 100 indicated very strong evidence; and values exceeding 100 signified extreme or decisive evidence.

For the linear and mixed linear models, we used a wide Cauchy prior distribution with r-scale (Rouder et al. 2012) value of 0.5 and tested the robustness of the results with additional scaling factors of 1 and $\sqrt{2}$. We used Normal (0, 1.5) priors for GLMM fixed effects as recommended in (McElreath 2018), and Normal (0, 2.5), and Normal (0, 10) for the priors sensitivity analysis.

2.13 Prediction models

We designed machine learning (ML) models to predict individual strategy usage based on physiological ET and behavioral measures. The models were computed with the scikit-learn (Pedregosa et al. 2011) library, Python 3.12.3.

A total of 10 path measures were used for all three VR modalities (detailed in section *2.9.2 Path measures*). For the two VR conditions, we additionally used 75 ET features consisting of 6 pupil features, 5 blinks features, and 4 groups of object-related features with 16 features in each group (see details in section *2.9.3 Eye-tracking measures*). The object groups included: the surrounding objects on the reward side of the maze (objects O_1, and O_2 in Fig.4 for example if the reward was on the right side), the surrounding objects on the opposite side to the reward (objects O_3, and O_4 in Fig.4 for example if the reward was on the right side), the cue on the reward side of the maze (the right arm of the maze in Fig. 4 for example if the reward was on the right side), and the cue on the opposite side to the reward (the left arm of the maze in Fig. 4 for example if the reward was on the right side). The scene design in the training phase determined the reference to the side of the reward of the objects and the cue for each participant.

All features were fed into support vector machine (SVM) models with radial basis function (RBF) classification or regression to predict the individual strategy usage. The models' performance was assessed using leave one subject out cross-validation (CV). On each fold, the missing values were first filled with the median of the features. Then, backward elimination feature selection was performed to decrease the number of features in the model and reduce the chance of overfitting. We constructed three categories of models as follows:

1. Trial-by-trial classification of the choice in strategy at each test probe trial based on the features extracted during that trial.
2. General preference of strategy classification based on the probability of using it calculated on all test probe trials as in Barnes *et al*. (Barnes et al. 1980). The models were fed with the median value of the features across all training trials or all trials.
3. Regression of the number of explicit choices in strategy. The models were fed with the median value of the features across all training trials or all trials.

The models' performance was assessed by accuracy for the classification models, and root mean square error (RMSE) and R^2 for the regression models. The statistical significance of the models' performance measures was assessed using permutation tests with 100 iterations. The permutation tests were performed only for models that obtained accuracy greater than 0.5 in the classification models, and R^2 greater than 0 in the regression models. Otherwise, the P-value was noted as 1.

This section was exploratory and was not preregistered.

3 Results

3.1 Learning measures

3.1.1 Learning pace

The average number of training trials required to reach 4 consecutive successes across all samples, conditions, and sessions was 7.8 trials. In the first sample, the learning pace in the 2D condition obtained a median of 10 trials to reach the learning criterion, which was significantly slower relative to a median of 6 trials in the VR walking condition (*estimate* = 23.3, $t_{(85.9)}$ = 2.6, *p* = 0.009, Fig. 5). Bayes factor analysis provided anecdotal evidence in favor of the alternative hypothesis with (BF10 = 1.8, 2,2, and 2.7 for the different prior scales). This result was not found in the second sample (*estimate* = 10.9, $t_{(144)}$ = 0.9, *p* = 0.36, Fig. 5c), with anecdotal support in favor of the null hypothesis (BF01 = 1, 1.2, and 1.2).

Contrast analysis showed, for the first sample, that during the first session, there was a significant difference in the learning pace between the 2D and VR walking conditions (*estimate* = -23.4, $t_{(85.9)}$ = -2.6, *p* = 0.027, Fig. 5a, Bonferroni corrected for 3 tests). This result was supported by anecdotal to moderate evidence with Bayes factor analysis (BF10 = 2.3, 3.3, and 4.1). The second sample did not obtain this result (*estimate* = -10.9, $t_{(144)}$ = -0.9, *p* = 1, Fig. 5c). Bayes factor analysis provided anecdotal evidence for the null (BF01 = 1.3, 0.9, and 1.3).

Another contrast found that for both samples the participants' learning pace was significantly faster in the second session compared to the first one in the 2D condition (*estimate* = 25.3, $t_{(43)}$ = 2.8, *p* = 0.007, for sample 1, Fig. 5a, and *estimate* = 36.6, $t_{(72)}$ = 3.1, *p* = 0.003, for sample 2, Fig. 5c, Bonferroni corrected for 3 tests). This suggests that familiarity with the 2D modality might have affected the learning pace in the first session in the 2D condition, which improved in the second session as participants gained experience.

Nevertheless, a main effect for the second session was not obtained (*estimate* = -14, $t_{(43)}$ = -1.6, *p* = 0.11), nor any of its interactions with the other experimental conditions (*estimate* = -11.3, $t_{(43)}$ = -0.9, *p* = 0.36) for Condition2D x Session2, and (*estimate* = 5.1, $t_{(43)}$ = 0.4, *p* = 0.67) for ConditionController x Session2, for the first sample. These results were replicated in the second sample with obtained (*estimate* = -12.3, $t_{(144)}$ = -1, *p* = 0.29) for the session main effect, and (*estimate* = -24.2, $t_{(144)}$ = -1.4, *p* = 0.15) for Condition2D x Session2, and (*estimate* = -2.1, $t_{(144)}$ = -0.1, *p* = 0.89) for ConditionController x Session2 interaction.

Eventually, there was no difference in the learning pace between the two VR conditions in the first sample (*estimate* = 4.2, $t_{(85.9)}$ = 0.5, *p* = 0.63), and in the second (*estimate* = -1.4, $t_{(144)}$ = -0.1, *p* = 0.91). Taken together, these results imply that there was no difference in the learning pace between the two VR conditions or the two sessions in these conditions, which suggests that the VR modalities were easier to adapt to than using the 2D interface.

3.1.2 Learning effectiveness

The success along the probe phases, on probe trials identical to training, was 79.5% success on average across all samples, conditions, and sessions. In the first sample, in the walking condition, participants obtained a median of maximum successful probe trials that were identical to training (9) which was significantly higher by 22.2% (2 trials) compared to 2D (*estimate* =-17.7, $t_{(85.4)}$ = -2.2, *p* = 0.033, Fig. 5b). Bayes factor analysis provided moderate support for the alternative hypothesis over the null (BF10 = 4, 6.8, and 8.7 for the different prior scales). This result was not replicated in the second sample (*estimate* = 0.5, $t_{(134.1)}$ = 0.04, *p* = 0.97, Fig. 5d) but with only anecdotal to no evidence of the null hypothesis over the alternative (BF01 = 1, 1.1, and 1.1).

Contrast analysis showed that during the second session, there was a significant difference in the learning effectiveness between the 2D and VR while walking conditions in the first sample (*estimate* =21.8, $t_{(85.4)}$ = -2.2, *p* = 0.03, Fig. 5b, Bonferroni corrected for 3 tests). This result obtained anecdotal evidence for the alternative hypothesis over the null (BF10 = 2.2, 1.8, and 2.3). The second sample did not obtain this result (*estimate* = -15.7, $t_{(134)}$ = -1.32, *p* = 0.57). Nevertheless, Bayes factor analysis found anecdotal to no evidence in the null hypothesis over the alternative (BF01 = 1, 1.1, and 1).

There was no significant difference in the learning effectiveness between the two VR conditions as a main effect for the controller condition in the first sample (*estimate* = -12.62, $t_{(85.4)}$ = -1.52, *p* = 0.13) or the second sample (*estimate* = 0.5, $t_{(134.1)}$ = 0.04, *p* = 0.97). In addition, there was no significant difference in the learning effectiveness between the two sessions, as a main effect (*estimate* = 4.75, $t_{(43)}$ = 0.61, *p* = 0.55) or as an interaction with the controller (*estimate* = 9.31, $t_{(43)}$ = 0.83, *p* = 0.41) or the 2D conditions (*estimate* = -3.88, $t_{(43)}$ = -0.35, *p* = 0.73). These results were replicated in the second sample with (*estimate* = -5.28, $t_{(134.1)}$ = -0.44, *p* = 0.66) for the controller main effect; (*estimate* = -0.32, $t_{(72)}$ = -0.03, *p* = 0.97) for the second session main effect; and (*estimate* = 15.2, $t_{(72)}$ = 1.06, *p* = 0.29) for the interaction of the second session with the 2D condition, and (*estimate* = 11.52, $t_{(72)}$ = 0.8, *p* = 0.42) with the controller condition.

The summary of the learning measures mixed linear models' results for each effect and sample is shown in Table A1 in the Supplementary material.

Fig. 5: Learning measures. Bar plots of learning measures per sample according to VR modality and session. Since the models were performed on the measures' ranks, the height of each bar presents the median, with error bars indicating ± 1 SEM (standard error of the mean). Individual data points are shown as dots overlaid on the bars, with y axis limit of mean ±2 SD (standard deviations). Top: The first sample's results. Bottom: The second sample's results. (p < 0.01 '**', p < 0.05 '*').

3.1.3 Learning strategy

Only 20.6% of all participants across both samples and all conditions explicitly chose only one strategy in both sessions. More than double of them chose only one strategy during one session (44.6% of both samples' participants). All other participants (55.4%) used a combination of strategies during the different probe trials and sessions.

Cue strategy: There was no significant effect for any of the fixed effects or interactions in the first sample for the probability of using cue strategy, as we preregistered. Indeed, no significant effect was obtained also in the second sample for the two experimental conditions with (OR = 0.45, 95% CI = [0.09, 2.16], and $p = 0.32$, and OR = 0.54, 95% CI = [0.18, 1.55], $p = 0.25$) for the 2D condition, and OR = 0.58, 95% CI = [0.12, 2.83], $p = 0.5$ and OR = 0.78, 95% CI = [0.27, 2.25], $p = 0.64$) for the controller condition in the first and second samples respectively.

Nevertheless, in the second sample, there was a significant main effect for the second session (OR = 0.39, 95% CI = [0.18, 0.82], $p = 0.014$), as well as interactions between the other conditions second session and the 2D and controller conditions (OR = 3.73, 95% CI [1.29, 10.81], $p = 0.015$) for Condition2D x Session2, and (OR = 3.25, 95% CI [1.11, 9.47], $p = 0.03$) for ConditionController x Session2. Bayes factor analysis found moderate to extreme evidence in favor of the null (BF10 = 0.3, 0.1, and 0) for the session main effect, moderate to anecdotal support in the alternative hypothesis for the interaction with the 2D condition (BF10 = 3.8, 3.2, and 1.1), and mixed anecdotal evidence in favor of the null and

alternative hypotheses for the interaction with the controller condition (BF10 = 2.3, 2, and 0.6). As mentioned above, these effects were not obtained in the first sample (OR = 1, 95% CI = [0.38, 2.62], p = 1) for the session main effect, (OR = 1.3, 95% CI = [0.32, 5.13], p = 0.71) for Condition2D x Session2, and (OR = 1.78, 95% CI = [0.43, 7.27], p = 0.74) for ConditionController x Session2 interaction. Bayes factor analysis showed strong to extreme evidence for the null for the session main effect (BF01 = 15.7, 56.2, and 3157.5), anecdotal to strong evidence for the null for the interaction with the 2D condition (BF01 = 2.3, 3.5, and 13.4), and anecdotal to moderate evidence for the null for the interaction with the controller condition (BF01 = 1.8, 2.5, and 9.3).

Contrast analysis revealed that in the second sample, the probability of using cue strategy significantly decreased in the second session relative to the first in the VR walking condition (OR = 2.57, 95% CI [1.2, 5.47], p = 0.014, Fig. 6b), with moderate to no support in the alternative hypothesis (BF10 = 4.3, 2.9, and 0.8). This result was also not obtained in the first sample (OR = 1, 95% CI [0.38, 2.63], p = 1, Fig. 6a), with moderate to strong evidence for the null (BF01 = 3.1, 5, and 19.4).

Place strategy: In the model for the probability of an explicit choice of place strategy a significant main effect of the second session was obtained in the first sample (OR = 3.84, 95% CI [1.38, 10.67], p = 0.009) as well as a significant interaction between session 2 and the VR using the controller condition relative to the model's default which was session 1 and the VR walking condition (OR = 0.11, 95% CI [0.02, 0.53], p = 0.006). Bayes factor analysis provided anecdotal to no support in the alternative model relative to the null for the second session main effect (BF10 = 2.5, 1.1, and 0 for the various priors SD), and strong to moderate evidence for the alternative hypothesis relative to null for the interaction (BF10 = 13.1, 15.9, and 6.5). These results were not obtained in the second sample (OR = 1.45, 95% CI [0.62,3.39], p = 0.39) for the session main effect and (OR = 0.46, 95% CI [0.15, 1.47], p = 0.18) for the session interaction with the controller condition. Bayes factor analysis showed strong to extreme evidence in favor of the null hypothesis (BF01 = 18.7, 66, and 3360) for the session main effect, and anecdotal to moderate evidence that supported null for the interaction with the controller (BF01 = 1.5, 2.1, and 7.5).

Contrast analysis revealed that the probability of using place strategy significantly increased in the second session relative to the first in the VR walking condition in the first sample (OR = 0.26, 95% CI [0.09, 0.72], p = 0.0098, Fig. 6a, Bonferroni corrected for 3 tests). In addition, during the second session, the probability of using the place strategy was higher in the VR walking condition relative to VR using the controller condition (OR = 8.5, 95% CI [1.33, 54.1], p = 0.016). Bayes factor analysis provided support to the alternative model, with moderate to strong evidence for the increase in the walking condition between the two sessions (BF10 = 11.7, 10, and 3.1) and anecdotal to moderate evidence for the difference between the two VR conditions in the second session (BF10 = 1.7, 2.9, and 3.2). None of these results were replicated in the second sample (OR = 0.68, 95% CI [0.29, 1.61], p = 0.39, Fig. 6b) for the sessions VR walking condition contrast, and (OR = 0.99, 95% CI [0.26, 3.88], p = 1, Bonferroni corrected for 3 tests) for the VR conditions contrast in the second session. Bayes factor analysis showed moderate to strong evidence for the null hypothesis, with (BF01 = 2.5, 4, and 16) for no difference between the sessions in the VR walking condition and (B01 = 2, 3.1, and 11.9) for the difference between the two VR conditions in the second session.

In both samples, the main effects for both conditions were not found, neither did the interaction of the second session with the 2D condition, with (OR = 1.42, 95% CI [0.34, 5.86], p = 0.63) and (OR = 2.22, 95% CI [0.72, 6.81], p = 0.16) for the 2D condition main effect in sample 1 and sample 2 respectively; (OR = 1.03, 95%CI [0.24, 4.37], p = 0.96) and (OR = 2.61, 95% CI [0.86, 7.98], p = 0.09) for the controller condition main effect in sample 1 and sample 2 respectively; and (OR = 0.43, 95% CI [0.1, 1.73], p = 0.23) (OR = 0.45, 95% CI [0.14, 1.46], p = 0.18) for the 2D interaction with session 2 in sample 1 and sample 2 respectively. This suggests that there was no difference in the probability of using place strategy between the two sessions for the 2D and controller conditions.

Response strategy: The probability for an explicit choice of response strategy (turn left/right) was significantly lower in the VR walking condition relative to both other conditions only in the first sample (OR = 4.92, 95% CI [1.24, 19.39], p = 0.03) and (OR = 9.63, 95% CI [2.42, 38.3], p = 0.001) for the VR controller and the 2D conditions respectively, Fig. 6a). Bayes factor analysis provided strong to moderate support in the alternative hypothesis (BF10 = 21.4, 19.6, and 6.3 for the different priors SD) for the 2D condition, and anecdotal to no support in the alternative model for the controller condition (BF10 = 2.9, 2.3, and 0.9). These results were not obtained for the second sample (OR = 0.86, 95% CI [0.27, 2.74], p = 0.8 and OR = 1.37, 95% CI [0.43, 4.35], p = 0.59, for the VR controller and the 2D conditions respectively, Fig. 6b). Bayes factor analysis found anecdotal to strong evidence in favor of the null (BF01 = 1.9, 3, and 12) for the controller condition, and (BF01 = 2.6, 3.8, and 17.3) for the 2D condition.

Contrast analysis showed that during the first session, the lower probability for using response strategy in the walking condition relative to 2D was significant (OR = 0.1, 95% CI [0.02, 0.56], p = 0.004, Fig. 6a, Bonferroni corrected for 3 tests) and it was marginal compared to using the controller (OR = 0.2, 95% CI [0.04, 1.1], p = 0.07). Bayes factor analysis showed moderate to strong evidence in favor of the alternative (BF10 = 9.7, 14.5, and 7.5) for the difference between the 2D and VR walking conditions in the first session. The contrast results were also not found in the second

sample (OR = 0.72, 95% CI [0.18, 2.97], *p* = 1, Fig. 6b, Bonferroni corrected for 3 tests), with anecdotal to strong evidence in favor of the null (BF01 = 2.1, 3, and 11.1).

Fig. 6: Choice of strategy. Bar plots of the number of explicit choices in each strategy during strategy test probe trials per sample according to VR modality and session. The height of each bar presents the mean, with error bars indicating ± 1 SEM. Individual data points are shown as dots overlaid on the bars. **a:** The first sample's results. **b:** The second sample's results. (p < 0.001 '***', p < 0.01 '**', p < 0.05 '*').

The session did not obtain a significant effect on the probability for using response strategy in both samples (OR = 1.37, 95% CI [0.45, 4.16], *p* = 0.57) and OR = 1.64, 95% CI [0.75, 3.59], *p* = 0.21) for the session main effect in the first and second samples respectively; (OR = 0.41, 95% CI [0.13, 2.48], *p* = 0.23) and (OR = 0.52, 95% CI [0.17, 1.75], *p* = 0.24) for the ConditionController x Session2 interaction in the first and second samples respectively; and (OR = 1.37, 95% CI [0.45, 4.16], *p* = 0.57) and OR = 1.64, 95% CI [0.75, 3.59], *p* = 0.21) for the Condition2D x Session2 interaction in the first and second samples respectively.

The summary of the choice of strategy generalized mixed linear models' results for each effect and sample is shown in Table A2 in the Supplementary material.

3.2 Eye-tracking measures

3.2.1 Pupil size

The pupils' behavior was assessed by the mean of the left pupil size in each trial (similar behavior was also observed for the right pupil data). The pupil size was significantly smaller in the second session (*estimate* = -0.14, $t_{(1180)}$ = -4.6, p = 3.3e-6, Fig. 7a) and (*estimate* = -0.05, $t_{(1938)}$ = -2, p = 0.04, Fig. 7c) in the first and second samples respectively. In both samples there was no main effect for condition (*estimate* = -0.05, $t_{(29.7)}$ = -0.3, p = 0.77) for sample 1, and (*estimate* = -0.14, $t_{(48.8)}$ = -0.8, p = 0.44) for sample2. However, an interaction between session and condition was obtained only in the second sample (*estimate* = -0.12, $t_{(1938)}$ = -3.5, p = 0.0004), and not in the first (*estimate* = -0.06, $t_{(1180)}$ = -1.4, p = 0.14). Contrast analysis showed that the pupil size decreased from the first session to the second in both VR conditions in both samples (*estimate* = 0.14, $t_{(1181)}$ = 4.7, p < 0.0001), and (*estimate* = 0.2, $t_{(1181)}$ = 6.8, p < 0.0001) for the walking and the controller conditions respectively for the first sample, Bonferroni corrected for 2 tests, Fig. 7a), and (*estimate* = 0.05, $t_{(1938)}$ = 2, p < 0.04), and (*estimate* = 0.17, $t_{(1937)}$ = 7.2, p < 0.0001) for the walking and the controller conditions respectively for the second sample, Bonferroni corrected for 2 tests, Fig. 7c). These results suggest that the pupils' size may slightly decrease after a few minutes in the VR headset, which could point to the participants' familiarity with the VR environment and adaptation to the display. (Kiefer et al. 2016; Iskander et al. 2019).

3.2.2 Blinks

We examined each trial's mean number of blinks to assess blink behavior. An interaction was obtained between the controller and the second session (*estimate* = -5.36, $t_{(1499)}$ = -3.5, p = 0.0004) in the first sample, but not in the second (*estimate* = 1.4, $t_{(2528)}$ = 1.2, p = 0.23). Nevertheless, in the second sample, a significant main effect was obtained for the second session (*estimate* = -2.06, $t_{(2530)}$ = -2.4, p = 0.018) and a marginal effect for the controller condition (*estimate* = 4.5, $t_{(53.2)}$ = 1.7, p = 0.09). Contrast analysis showed a decrease in the number of blinks from the first session to the second in the controller condition in the first sample (*estimate* = 4.14, $t_{(1500)}$ = 3.8, p = 0.0001, Bonferroni corrected for 2 tests, Fig. 7b) but not in the second (*estimate* = 0.62, $t_{(2526)}$ = 0.7, p = 0.47). On the hand, a significant decrease in the number of blinks from the first session to the second was found in the walking condition in the second sample (*estimate* = 2.06, $t_{(2530)}$ = 2.4, p = 0.018, Bonferroni corrected for 2 tests, Fig. 7d) but not in the first (*estimate* = -1.19, $t_{(1499)}$ = -1.1, p = 0.27, Bonferroni corrected for 2 tests, Fig. 7b). Moreover, only in the second sample, smaller number of blinks were observed in the second session in the walking condition compared to the controller (*estimate* = -5.95, $t_{(53.8)}$ = -2.2, p = 0.03, Bonferroni corrected for 2 tests), but not in the first sample (*estimate* = 2.5, $t_{(32.1)}$ = 0.7, p = 0.47, Bonferroni corrected for 2 tests).

The summary of the ET measures mixed linear models' results for each effect and sample is shown in Table A3 in the Supplementary material.

3.2.3 Visual attention measured by gaze time

We speculated whether there was a difference in the visual attention given to the different objects in the scene in the two VR conditions. To address this, we considered the percent time objects were gazed out of each entire trial duration.

Gaze time at cue on the reward side: The percent time gaze at the cue on the reward side was 5.6% and 4.6% on average in the first and second samples respectively. In both samples, it showed no significant main effects (*estimate* = -0.32, $t_{(41)}$ = -0.4, p = 0.7), and (*estimate* = 0.03, $t_{(929)}$ = 0.05, p = 0.96) for the condition and session main effects in the first sample, and (*estimate* = -0.13, $t_{(59)}$ = -0.2, p = 0.86), and (*estimate* = -0.39, $t_{(1327)}$ = -0.9, p = 0.35) in the second sample. Nevertheless, an interaction of the condition and the session number was obtained in the second sample (*estimate* = 1.69, $t_{(1324)}$ = 2.9, p = 0.004, Fig. 8c), even though it was not observed in the first (*estimate* = -0.93, $t_{(925)}$ = -1.25, p = 0.23, Fig. 8a). Contrast analysis for the second sample showed that the percent time the cue on the reward side was gazed at in the controller condition in the second session was significantly higher relative to the first session (*estimate* = -1.3, $t_{(1320)}$ = -3.2, p = 0.0014, Bonferroni corrected for 2 tests, Fig. 8c), and to the walking condition in the second session (*estimate* = -1.6, $t_{(72.7)}$ = -2, p = 0.046, Bonferroni corrected for 2 tests).

Gaze time at surrounding objects on the reward side: The average percent time the surrounding objects on the reward side were gazed at was 5.1% and 4.8% in the first and second samples respectively (objects O_1, and O_2 in Fig. 4 for example if the reward was on the right side). It was significantly lower by 1.9% in the controller condition relative to walking in the first sample (*estimate* = -1.9, $t_{(46)}$ = -2.5, p = 0.014) and by 1.5% in the second sample (*estimate* = -1.53, $t_{(66.6)}$ = -2.4, p = 0.02). In the first sample, a significant main effect was obtained for the second session (*estimate* = 0.9, $t_{(770)}$ = 2.1, p = 0.03), but not in the second sample (*estimate* = -0.31, $t_{(1182)}$ = -0.9, p = 0.37). On the other hand, an interaction was obtained in the second sample (*estimate* = 1.53, $t_{(1187)}$ = 2.9, p = 0.004), and not in the first sample (*estimate* = -0.56, $t_{(771)}$ = -0.8, p = 0.4). Contrast analysis found that the percent time the objects on the reward side were gazed at significantly increased from the first session to the second in the walking condition in the first sample (*estimate* = -0.9, $t_{(770)}$ = -2.1, p = 0.03, Bonferroni corrected for 2 tests, Fig. 8a), but not in the second sample (*estimate* = 0.31, $t_{(1180)}$ = 0.9, p = 0.37).

Nevertheless, this increase was observed in the controller condition in the second sample (*estimate* = -1.22, $t_{(1190)}$ = -3, *p* = 0.002, Bonferroni corrected for 2 tests, Fig. 8c), and not in the first sample (*estimate* = -0.34, $t_{(772)}$ = -0.7, *p* = 0.5). In addition, in the first sample, in both sessions, the percent time the objects on the reward side were gazed at, was significantly higher in the walking condition compared to the controller (*estimate* = 1.9, $t_{(43.8)}$ = 2.5, *p* = 0.014) and (*estimate* = 2.5, $t_{(44.1)}$ = 3.3, *p* = 0.002) for the first and second sessions respectively, Bonferroni corrected for 2 tests). This result was replicated in the second sample only in the first session (*estimate* = 1.52, $t_{58.9}$ = 2.4, *p* = 0.02), and not the second (*estimate* = -0.005, $t_{(71.1)}$ = -0.007, *p* = 0.99). Taken together, these results suggest that during the first few moments of engaging in the task, participants paid more attention to the surrounding objects in the reward side in the walking condition compared to moving with the controller. In addition, there may be an increase in the visual attention given to these objects in each modality, in the second session.

Fig. 7: Eye-tracking (ET) measures. Bar plots of ET measures according to VR modality. The height of each bar presents the mean, with error bars indicating ± 1 SEM. Individual trial-based data points are shown as dots overlaid on the bars. Top: The first sample's results. Bottom: The second sample's results. (p < 0.001 '***', p < 0.01 '**', p < 0.05'*').

Gaze time at all surroundings objects: Participants gazed at all the surrounding objects 8.3% and 7.6% on average out of each trial duration in the first and second samples respectively (objects $O_1 - O_5$ in Fig. 4). The percent time all the objects were gazed at was significantly lower in the controller condition compared to walking by 40% (*estimate* = -3.3, $t_{(39)}$ = -3.1, *p* = 0.003) in the first sample, and by 30% (*estimate* = -2.26, $t_{(58)}$ = -2.2, *p* = 0.03) in the second. In both samples, there was no difference between the two sessions (*estimate* = -0.06, $t_{(1058)}$ = -0.1, *p* = 0.91), nor an interaction with condition (*estimate* = -0.01, $t_{(1059)}$ = -0.02, *p* = 0.98) for sample 1, and (*estimate* = 0.1, $t_{(1642)}$ = 0.2, *p* = 0.8) and (*estimate* = 0.64, $t_{(1645)}$ = 1, *p* = 0.32) for sample 2. Contrast analysis found this effect in both sessions (*estimate* = 3.3, $t_{(38.1)}$ = 3.1, *p* = 0.003 and (*estimate* = 3.3, $t_{(40)}$ = 3.1, *p* = 0.004) for the first and second sessions respectively, Bonferroni corrected for 2 tests, Fig. 8a) in the first sample, and only in the first session in the second sample (*estimate* = 2.26, $t_{(55.1)}$ = 2.2, *p* = 0.03), and (*estimate* = 1.26, $t_{(60.6)}$ = 1.5, *p* = 0.14, Bonferroni corrected for 2 tests, Fig. 8c). Suggesting that, the attention given to

the surrounding objects as a group was higher in the first session in walking conditions compared to standing in place and using the controller.

The summary of the visual attention measured by gaze time mixed linear models' results for each effect and sample is shown in Table A4 in the Supplementary material.

Fig. 8: Gaze behavior measures. Bar plots of the percent time objects were gazed per trial according to VR modality. The height of each bar presents the mean, with error bars indicating ± 1 SEM. Individual trial-based data points are shown as dots overlaid on the bars. **a:** The first sample's results. **b:** The second sample's results. ($p < 0.001$ '***', $p < 0.01$ '**', $p < 0.05$'*').

3.3 Identification of individual strategy usage based on eye tracking and path features

Since differences in the ET features were observed between sessions, conditions, and samples (see section *3.2 Eye-tracking measures*), for each category and data type, a model was constructed for each strategy, session, condition, and sample. The results are detailed in the Supplementary material in tables A5-A14.

In the attempt to predict the strategy used in each strategy test probe trial in sample 1, a trend accuracy of 0.6 was obtained for the place strategy in the second session ($p = 0.069$). Nevertheless, in the second sample, significant results were obtained for classification in the walking condition in the second session for place (*accuracy* = 0.76, $p = 0.04$), and response (*accuracy* = 0.64, $p = 0.05$) and in the first session for response using the controller (*accuracy* = 0.69, $p = 0.02$).

Predicting whether the cue strategy was the preferred one in sample 1 obtained an accuracy of 0.75 in the walking condition for the first session in sample 1 ($p = 0.04$) based on the training trials' data, and an accuracy of 0.81 based on all trials data ($p = 0.03$). However, in the walking condition in the second sample, a significant accuracy of 0.72 was obtained for the response strategy in the second session ($p = 0.05$) when using only training trials, and an accuracy of 0.68 for the cue strategy when we used data from all the trials ($p = 0.05$).

Finally, regression for the number of explicit choices in strategy in the first sample in the walking condition provided with ($R^2 = 0.2$, $RMSE = 1.07$, $p = 0.04$) for the cue strategy in the second session when using only the training trials data, and ($R^2 = 0.4$, $RMSE = 0.67$, $p = 0.01$), and ($R^2 = 0.43$, $RMSE = 0.7$, $p = 0.04$) for the response strategy in the first and second sessions respectively when using all the data. In the second sample, regression to the number of choices of cue strategy obtained ($R^2 = 0.17$, $RMSE = 1.02$, $p = 0.04$) in the first session using the controller when only training trials were used, and ($R^2 = 0.08$, $RMSE = 1.2$, $p = 0.04$) in the 2D condition, and ($R^2 = 0.37$, $RMSE = 0.84$, $p = 0.01$) for place in the walking condition both in the second session when all trials were used.

Taken together, even though the classification and regression results generally vary between sessions, strategies, experimental conditions, and samples, most of the significant models (all in sample 1) were obtained for the walking condition, and only one in the 2D condition, and most in sample 2 were for session 2.

3.4 Presence measures

3.4.1 Spatial presence

In the first sample, a significantly higher sense of spatial presence was obtained in the VR walking condition relative to the 2D condition (*estimate* = -13.4, $t_{(43)} = -3$, $p = 0.004$, Fig. 9a). Contrast analysis showed a significantly lower sense of spatial presence in the 2D condition relative to both VR conditions (*estimate* = 13.4, $t_{(43)} = 3$, $p = 0.01$, and *estimate* = -13, $t_{(43)} = -2.9$, $p = 0.02$ for walking and controller conditions respectively, Bonferroni corrected for 3 tests). These results were replicated in the second sample (*estimate* = -28.2, $t_{(72)} = -5.4$, $p = 8.6e-7$, *estimate* = 28.2, $t_{(72)} = 5.38$, $p < 0.0001$, and *estimate* = -19.9, $t_{(72)} = -3.8$, $p = 0.0009$ respectively, Fig. 9b). In both samples, there was no significant difference in the sense of spatial presence between the two VR conditions (*estimate* = -0.3, $t_{(43)} = -0.07$, $p = 0.94$, and *estimate* = -8.3, $t_{(72)} = -1.59$, $p = 0.12$, for the first and second samples respectively).

3.4.2 Engagement

In addition, a significantly higher sense of engagement was found in the first sample in the VR walking condition relative to the 2D condition (*estimate* = -10.6, $t_{(43)} = -2.3$, $p = 0.03$). Contrast analysis showed a marginally higher sense of engagement in the VR walking condition relative to the 2D condition (*estimate* = 10.6, $t_{(43)} = 2.3$, $p = 0.08$, Bonferroni corrected for 3 tests). These results were replicated in the second sample (*estimate* = -22.9, $t_{(72)} = -4.2$, $p = 8.8e-5$). Contrast analysis on the second sample found a significantly lower sense of engagement in the 2D condition relative to both VR conditions (*estimate* = 22.9, $t_{(72)} = 4.16$, $p = 0.0003$, and *estimate* = -20.1, $t_{(72)} = -3.6$, $p = 0.0015$ for walking and controller conditions respectively, Bonferroni corrected for 3 tests, Fig. 9b). Bayes factor analysis for the 2D-controller contrast showed moderate to strong evidence in favor of the alternative (BF10 = 7.1, 13, and 17.8). This difference was not found in the first sample (*estimate* = -6.3, $t_{(43)} = -1.3$, $p = 0.56$) with equal support for both hypotheses (BF01 = 1 for all prior scales). Eventually, no significant difference was found between the two VR conditions for this factor as well (*estimate* = -4.3, $t_{(43)} = -0.9$, $p = 0.36$, and *estimate* = -2.8, $t_{(72)} = -0.51$, $p = 0.61$, for the first and second samples respectively).

3.4.3 Ecological validity/naturalness

The ecological validity/ naturalness of the environment was also found to be significantly higher in the VR walking condition relative to the 2D condition (*estimate* = -10.1, $t_{(43)} = -2.2$, $p = 0.03$) in the first sample. Contrast analysis revealed that the sense of ecological validity in the 2D condition was significantly lower relative to the VR controller condition (*estimate* = -12.4, $t_{(43)} = -2.7$, $p = 0.03$, Fig. 9a), and marginally lower relative to the VR walking condition (*estimate* = 10.1, $t_{(43)} = 2.2$, $p = 0.09$, Bonferroni corrected for 3 tests). These results were replicated in the second sample (*estimate* = -23.4, $t_{(72)} = -4.2$, $p = 6.7e-5$, *estimate* = -18.2, $t_{(72)} = -3.28$, $p = 0.005$, and *estimate* = 23.4, $t_{(72)} = 4.2$, $p = 0.0002$ respectively, Fig. 9b). There was no observed difference between the two VR conditions also for the ecological validity (*estimate* = -2.3, $t_{(43)} = 0.5$, $p = 0.61$, and *estimate* = -5.3, $t_{(72)} = -0.95$, $p = 0.34$, for the first and second samples respectively).

3.4.4 Negative effects

Since no significant effects were found regarding the negative effects factor derived from the presence questionnaire in the first sample (Fig. 9a), we did not preregister them. Nevertheless, as they were observed in the second sample, they are included in this scope. Significantly higher negative effects were obtained for the VR walking condition relative to 2D in the second sample (*estimate* = -29, $t_{(72)} = -5.6$, $p = 3.65e-7$) and marginally higher than the controller (*estimate* = -9.7, $t_{(72)} = -1.9$, $p = 0.06$). Contrast analysis found significantly lower negative effects in the 2D condition relative to both VR conditions (*estimate* = 29, $t_{(72)} = 5.6$, $p < 0.0001$, and *estimate* = 28.2, $t_{(72)} = -19.34$, $p = 0.001$ for walking and controller conditions respectively, Bonferroni corrected for 3 tests, Fig. 9b). Bayes factor analysis indicated extreme evidence in favor of the alternative hypothesis for the 2D - walking contrast (BF10 = 1078, 2140, and 3028), and

moderate to strong evidence for the 2D - controller contrast (BF10 = 8, 15.1, and 20.4). As noted above, these results were not found in the first sample (*estimate* = -5.3, $t_{(43)}$ = -1.1, *p* = 0.27, *estimate* = 5.3, $t_{(43)}$ = 1.1, *p* = 0.82, *estimate* = -6.5, $t_{(43)}$ = -1.3, *p* =0.57, for the 2D - walking main effect, 2D - walking contrast, and 2D - controller contrast respectively), with non to anecdotal support in the null (BF01 = 1, 1.1, and 1.1 for both contrasts). As preregistered, there was no difference in the negative effects between the two VR conditions in the first sample (*estimate* = 1.2, $t_{(43)}$ = 0.2, *p* = 0.81).

The summary of the presence questionnaire factors linear models' results for each effect and sample is shown in Table A15 in the Supplementary material.

Fig. 9: Sense of presence. Bar plots of presence factors according to VR modality. The height of each bar presents the median, with error bars indicating ± 1 SEM. Individual data points are shown as dots overlaid on the bars. **a:** The first sample's results. **b:** The second sample's results. (p < 0.001 '***', p < 0.01 '**', p < 0.05'*').

3.5 Awareness measures

There was a significant positive relation between the perception of using the cue strategy and the number of choices of it (*estimate* = 0.6, $t_{(38)}$ = 2.7, *p* = 0.009) and (*estimate* = 0.54, $t_{(66)}$ = 2.5, *p* = 0.014) for the perception of strategy main effect in the first and second samples respectively.

As for place strategy, a significant positive relation between the perception of using it and the actual number of choices of it was found only in the first sample (*estimate* = 0.65, $t_{(38)}$ = 2.5, *p* = 0.018), with (*estimate* = 0.1, $t_{(66)}$ = 0.4, *p* = 0.72) for the second sample. Bayes factor analysis indicated significant to anecdotal evidence for the alternative hypothesis for sample 1 (BF10 = 13.6, 4.3, and 2) and no support to moderate in the null for the second sample (BF01 = 0.8, 2.8, and 6.2).

An interaction was found between the perception of using the response strategy and the controller condition in the first sample (*estimate* = 0.75, $t_{(38)}$ = 2.3, *p* = 0.03) with moderate to no evidence for the alternative (BF10 = 2.6, 1.4, and 1). Nevertheless, in the second sample, a marginal main effect was obtained (*estimate* = 0.38, $t_{(66)}$ = 1.8, *p* = 0.07), and no interaction was obtained (*estimate* = -0.14 $t_{(66)}$ = -0.48, *p* = 0.63) with moderate support in the null (BF01 = 3,4.6, and 6). Even though we did not preregister the effect for each modality, we explored each modality separately due to the obtained interaction. The analysis revealed that in the first sample perception of using response strategy was a significant predictor of the actual choices of it in both the controller and 2D conditions, with a slightly stronger effect for the controller (*estimate* = 0.89, $t_{(38)}$ = 3.8, *p* < 0.001) than the 2D (*estimate* = 0.65, $t_{(38)}$ = 3.1, *p* = 0.003), and not for the walking condition (*estimate* = 0.14, $t_{(38)}$ = 0.63, *p* = 0.53). Notwithstanding, in the second sample, the perception of using the response strategy was significantly positively related to the number of choosing it in the 2D condition (*estimate* = 0.55, $t_{(66)}$ = 2.65, *p* = 0.01), marginally in the walking condition (*estimate* = 0.38, $t_{(66)}$ = 1.82, *p* = 0.07), and not related in the controller condition (*estimate* = 0.24, $t_{(66)}$ = 1.16, *p* = 0.25). This results in a significant relation in the 2D condition in both samples.

The awareness level of the strategies information was not related to the actual choices of them in both samples (p > 0.2 in all models for all strategies for main effects and interactions with the experimental conditions, the models' results are detailed in the Supplementary material in Tables A16-A21). The participants were aware of the information of the strategies in the scene (the 99th percentile of the awareness ranks was maximal (3) for all strategies and VR modalities. When considered alongside the models' results, this implies that not choosing a strategy was not a result of being unaware

of the information it held.

The summary of the relation between the perception of using strategy, and the awareness of strategy information to the number of choices linear models' results for each effect and sample are shown in Tables A22-A23, and Fig. A1 -A2 in the Supplementary material.

3.6 Spatial abilities measures

3.6.1 MRT

The MRT score was not related to the number of choices in any strategy (*estimate* = -0.09, $t_{(69)}$ = -0.4, *p* = 0.68) for cue, (*estimate* = -0.08, $t_{(69)}$ = -0.4, *p* = 0.68 for place, and (*estimate* = -0.08, $t_{(69)}$ = -0.4, *p* = 0.68) for response. In addition, no interaction was obtained with the VR modality (*p* > 0.3 for all conditions and strategies, the models' results are detailed in Tables A24-A26, and Fig. A3 in the Supplementary material).

3.6.2 SOT

The SOT score was not related to the number of choices in cue strategy (*estimate* = -0.16, $t_{(69)}$ = -0.9, *p* = 0.39), and in place strategy (*estimate* = 0.27, $t_{(69)}$ = 1.5, *p* = 0.13). Nevertheless, there was a marginally significant relation of the SOT score to the number of choices in response strategy (*estimate* = 0.33, $t_{(69)}$ = 1.8, *p* = 0.07). Here as well, no interaction was observed with the VR modality (*p* > 0.17 for all conditions and strategies, the models' results are detailed in Tables A27-A29, and Fig. A3 in the Supplementary material).

3.7 Demographic data

3.7.1 Sex

There was no difference in the sex distribution between the two samples (*estimate* = -0.09, $t_{(115)}$ = -0.6, *p* = 0.53) for the sample main, or any of the interactions with the VR modality (p > 0.6 for both interaction terms).

3.7.2 Age

There was also no age difference between the two samples (*estimate* = 1, $t_{(115)}$ = 0.59, *p* = 0.55) for the sample main effect or any of the interactions with the VR modality (p > 0.8 for both interaction terms).

3.7.3 Past VR experience

There was a marginal effect of the sample on the past VR experience (*estimate* = 0.27, $t_{(115)}$ = 1.9, *p* = 0.06), and a significant interaction with the controller condition group (*estimate* = -0.48, $t_{(115)}$ = -2.3, *p* = 0.02). Contrast analysis found a marginally higher number of participants with past VR experience in the second sample compared to the first in the VR walking group (*estimate* = -0.27, $t_{(115)}$ = -1.9, *p* = 0.06, Bonferroni corrected for 3 tests).

3.7.4 Frequency of playing computer games

There was no difference in the frequency of playing computer games between the two samples (*estimate* = 0.01, $t_{(115)}$ = 0.03, *p* = 0.98) for the sample main effect, or any of the interactions with the VR modality (p > 0.5 for both interaction terms).

4 Discussion

This study aimed to investigate how different levels of immersion of VR modalities, their locomotion interfaces, and proprioception influence spatial learning measures, particularly strategy selection. For this purpose, to the best of our knowledge, we translated for the first time the classic T-maze task from (Barnes et al. 1980) to humans, aimed to disentangle three possible learning strategies: cue, place, and response. Using this paradigm, we compared three conditions: 3D HMD VR with physical walking, 3D HMD VR with controller-based movement, and 2D desktop VR with mouse and keyboard navigation. In addition, by leveraging the built-in eye-tracker in the two HMD VR conditions, we assessed whether VR modality level of immersion and locomotion methods influence visual attention during spatial navigation and its relationship to strategy usage. Lastly, we sought the predictive potential of ET data for strategy identification across walking and controller-based VR conditions and attempted to predict strategy usage both globally and on a trial-by-trial basis. Our results, obtained on two samples, provide several key insights into human spatial navigation, gaze behavior, and the impact of VR modalities on spatial learning.

4.1 Translation of the T-maze task to humans

The T-maze task was effectively adapted to humans in all VR modalities. This was demonstrated by the participants' ability to encode navigating to the reward by reaching the task's learning criteria (4 consecutive successful trials in the training session, like the original study). Human participants fulfilled the learning criterion nearly twice as fast as the rodents in (Barnes et al. 1980). This is of course in line with the realization that the T-maze task is indeed a rather simple task for humans relative to rodents.

Nearly 80% success was achieved in probe trials that were identical to training, which implies that the participants remembered the learned scheme during the probe phase as well. Since each test probe trial was preceded and followed by these regular probe trials, this result suggests that the participants' choice of strategy in the test probe trials was not derived from a new encoding of the test trials design.

In correspondence to the original study in rodents, different participants employed all place, response, and cue strategies when navigating the virtual T-maze in all VR modalities. In the original study (Barnes et al. 1980), both young and older rats showed a general preference for response strategy, with a between-group interaction, where the older rodents chose the simpler response strategy over place strategy compared to the younger rats. Similarly, our human participants also demonstrated a general tendency to use one of the S-R strategies, but differently than the rodents, they used the cue strategy more than the two others.

Across all conditions, we observed that most participants employed a mixture of place, response, and cue strategies when navigating the virtual T-maze between the two sessions and even within a session. About half of the participants who used only one strategy in each session changed it in the second session. This finding aligns with previous research demonstrating the flexibility of navigation strategies in the plus maze paradigm in rodents (Packard and McGaugh 1996) and humans (de Condappa and Wiener 2016), as well as in Tolman's sunburst translation to humans (Doner et al. 2023).

4.2 Impact of VR modality on spatial learning performance

Learning performance (pace and effectiveness) showed no significant differences between the two immersive VR conditions utilizing physical walking and controller-based movement. This finding contributes to an ongoing discussion in the field of spatial cognition regarding the impact of different VR modalities and proprioception on navigation performance. On the one hand, (Huffman and Ekstrom 2019) found no significant behavioral differences in pointing accuracy, rate of learning, or spatial memory performance suggesting that spatial retrieval tasks are modality-independent across different VR levels of body-based and joystick movement, supporting our results. On the other hand, (Ruddle et al. 2011) found that proprioceptive feedback significantly improved the accuracy of cognitive maps in VR environments. These contrasting findings suggest that the effect of VR modality on spatial learning may be task-dependent and warrants further investigation across various spatial navigation paradigms.

The significant difference in learning performance between the 2D and VR walking conditions was only observed in the first sample. Bayes factor analysis showed anecdotal to no support for the corresponding hypothesis in each sample, suggesting that a larger sample size would be required for conclusive results. This discrepancy between the two samples could also be attributed to our increased attention and detailed explanation of how to use the mouse and keyboard for navigation in the second sample. The results of the second sample are supported by previous research. A comparison of HMD VR and desktop versions of an 8-arm RAM found no significant differences in performance between the two modalities (Kim et al. 2018), and no differences were reported also when three strategies were tested in a virtual sunburst maze (Doner et al. 2023).

Notably, the learning pace in the 2D condition increased significantly from the first session to the second in both samples. This suggests that participants required time to familiarize themselves with the modality, which initially affected their learning pace. This effect diminished as they became accustomed to the interface in the second session. Since we aimed to test and reveal the effect VR modality has on spatial learning characteristics, unlike most studies, our experiment began the training trials immediately, without any practice time for navigating the environment. This allowed us to engulf the effect of modality habituation and naturalness of use on learning. Our results demonstrate the importance of considering learning effects when comparing different VR modalities and emphasize the need for adequate training periods in spatial navigation studies, where natural habituation wasn't a research question like in our case. Given that most studies typically include a practice period for participants to familiarize themselves with the navigation controls before the actual experiment begins, reporting the average amount of time it requires could contribute greatly to the field.

4.3 Impact of VR modality on spatial learning strategy

Examination of strategy usage across different VR modalities revealed that in both samples, there were no significant differences in the probability of using any strategy between the 2D and the VR controller conditions, and between all modalities for the cue strategy. Nevertheless, in the first sample in the VR walking condition participants chose the response strategy significantly less than in the two other conditions and chose place strategy significantly more than the controller in the second session. A group effect of a change between the two sessions, that required encoding of a new setup relative to the first, was observed only in the VR walking condition. We found an increase in using place strategy in the first sample and a decrease in using cue strategy in the second. Most of these results correspond to insights from (Doner et al. 2023), where no differences were reported between modalities for strategy usage, even though flexibility in strategy selection was observed within each modality.

The lack of consistent findings across samples was supported by Bayes factor analysis of the corresponding effects to various degrees, with some Bayes factors classified as anecdotal, emphasizing the need for larger double in size participant groups to accumulate more evidence in favor of one hypothesis over the other. Additional factors likely contributed to these inconsistencies, including the small effect sizes observed, the relatively modest statistical significance of some effects (p-values exceeding 0.001), and the variability in strategy usage within participants. Furthermore, the differences in instructional emphasis between samples, particularly for the 2D and controller groups in the second sample, may have further influenced the observed discrepancies. Finally, the sample size of the second group was determined by power analysis to achieve 80% power, which inherently leaves a 20% chance of failing to replicate effects even though they may exist in the population.

We additionally analyzed demographic data to assess possible factors for the variety in some of the samples' results. There were no differences between the samples for sex, age, and frequency of playing computer games. A marginally significantly higher past VR experience was observed in the second sample compared to the first, particularly in the VR walking group. This difference in VR familiarity could potentially contribute to the variability in results between the two samples. For some participants, the experience with VR could be with gaming. Therefore, since gaming experience has been associated with improved spatial abilities and navigation performance in virtual environments (Richardson et al. 2011), these subtle demographic differences could partially explain the inconsistencies observed between the two samples in strategy usage and learning measures.

These results highlight individual variability in strategy utilization, and the potential that gaze behavior analysis may provide for deeper insights into the mechanisms driving strategy usage.

4.4 Pupil size and blink rate

Interestingly, pupil size decreased significantly from the first session to the second across both conditions and samples. This consistent finding may reflect participants' adaptation to the VR display over time (Kiefer et al. 2016; Iskander et al. 2019), potentially reducing cognitive load or visual strain. Previous research has shown that pupil size can be influenced by factors such as cognitive load, emotional arousal, and visual adaptation (Mathôt 2018). In our case, the decrease might reflect reduced cognitive effort as participants become more familiar with the task and environment. Such adjustments have been reported in prior spatial learning studies linking pupil size to task engagement and cognitive demands (de Condappa and Wiener 2016). However, the implications of this change remain speculative and warrant further investigation to understand its relationship to navigation strategy and VR adaptation.

One area of inconsistency was blink behavior, where results varied between samples and conditions. Blink rate has been associated with various cognitive processes, including attention, cognitive load, and fatigue (Stern et al. 1994). The inconsistency in our findings suggests that the blinks' role in spatial navigation tasks may be influenced by factors beyond cognitive demands, such as VR-specific visual strains or individual variability in blink patterns.

4.5 Visual attention to maze cues

One of our primary goals was to assess whether visual attention to maze cues differed between VR modalities and sessions. Our findings revealed consistent patterns across both samples, particularly in the first session. Participants in the walking condition spent significantly more time gazing at objects on the reward side and the entire set of surrounding objects compared to those in the controller condition. This suggests that physical walking, being a more natural form of locomotion for humans, may allow for greater allocation of attention to environmental cues. In contrast, the need to adapt to controller-based movement may initially reduce attention to the environment. This interpretation is supported by a study (Drewes et al. 2021), that found several gaze features affected by the experimental condition of real-world navigation compared to controller-based VR, reflecting altered visual exploration due to VR constraints. Furthermore, the increased

attention to reward-side objects during walking reinforces the importance of task immersion and locomotion modality in shaping gaze behavior.

The increase in gaze time on the objects in the reward-side from the first to the second session in the walking condition, and when comparing the two VR conditions in the first sample, may reflect an interplay between behavioral choices in strategies and visual attention. However, it is important to note that these patterns were not entirely consistent across samples, highlighting the potential for individual differences in visual exploration strategies. This variability in gaze behavior may also stem from the employment of a mix of strategies, as observed by many participants. This aligns with previous findings (de Condappa and Wiener 2016), that noted mixed gaze behaviors in navigation tasks, reflecting the interplay of multiple strategies. This variability underscores the importance of using multiple ET features in our predictive models to capture the full range of gaze behaviors.

4.6 Prediction of navigation strategies

Our attempts to predict navigation strategies based on ET and behavioral data yielded mixed results. While classification models showed some success in identifying strategy usage, their accuracy varied across strategies, conditions, and sessions. For instance, predicting strategy choice was more successful in the walking condition, suggesting that physical locomotion may elicit more distinct gaze and behavioral patterns conducive to strategy identification.

The accuracy of our models varied depending on whether we used data from all trials, training trials only, or single trials. This variability corresponds with our finding that most participants did not rely exclusively on a single strategy but employed a mix of strategies throughout the task. As mentioned above, this finding aligns with previous research (de Condappa and Wiener 2016) that examined three possible strategies and also observed mixed gaze behavior associated with different navigation strategies. Interestingly, although the T-maze paradigm may seem as a simple task for human subjects, it elicited complex behavior.

The challenge in predicting strategies may also be due to the relatively small number of probe trials in our design compared to traditional classification tasks. Additionally, the unbalanced class distributions across some of the strategies likely influenced model performance and statistical significance of our results, even when accuracy was relatively high. Future studies could benefit from larger sample sizes, and from incorporating more probe trials to obtain more data for each participant and between participants.

4.7 Awareness of strategy usage across VR modality

The relationship between participants' perception of strategy usage and their actual choices during the task was significantly correlated across all conditions for the cue strategy in both samples and the place strategy in the first sample, indicating that participants were generally aware of their reliance on these strategies. However, for the response strategy, this positive correlation was found in the 2D condition in both samples, the VR controller condition in the first sample, and the VR walking condition in the second sample. Interestingly, in the VR conditions participants often perceived that they used the response strategy even when their actual behavior indicated otherwise. This discrepancy suggests that participants may conflate the concept of habitual turns with more complex navigation strategies, or they may recall their intended actions rather than their actual choices during navigation. The dissociation between the perception of using strategy and behavior, particularly for the response strategy, aligns with the idea that spatial navigation often involves implicit learning processes, as suggested by (Chrastil and Warren 2014).

The analysis of participants' reported awareness of the information of each strategy, and actual strategy implementation add to these intriguing findings. While participants generally reported high awareness of the spatial or motoric cues associated with each strategy across modalities and samples, their explicit choices during the task were not associated with it. This implies that choices in one strategy were not derived by not noticing the other strategies.

These findings echo previous findings (Lawton 1994), where self-reported navigation strategies often aligned with spatial perception ability but were not always predictive of observed behaviors. Similarly, another study (Bray et al. 1999) noted strong correlations between self-reports and observed strategies but highlighted cases of implicit strategy use that participants failed to report. Our structured approach, where participants selected their perceived strategy from a predefined scale, contrasts with other studies (Kim et al. 2018; Gammeri et al. 2022), which utilized verbal reports.

Furthermore, the use of multiple strategies by many participants across sessions and probe trials likely contributed to the variability in the relationship between awareness, perception, and behavior. These findings emphasize the value of combining objective behavioral measures with subjective reports to capture the full complexity of spatial learning strategies, particularly in immersive and dynamic environments.

4.8 Presence and ecological validity

The analysis of presence factors showed significantly higher ratings of spatial presence, engagement, and ecological validity in both HMD VR conditions compared to the 2D desktop condition in both samples. This aligns with previous research demonstrating the benefits of immersive VR for creating more ecologically valid experimental environments compared to 2D displays (Kim et al. 2018). The enhanced sense of presence in HMD VR may contribute to more effective spatial learning by providing a more realistic context for encoding spatial information.

Interestingly, we did not observe significant differences in any of the presence measures between the two HMD VR conditions (walking vs. controller-based movement), also in congruence with previous findings (Kim et al. 2018). This suggests that the immersive visual experience provided by HMD VR may be more critical for creating a sense of presence than the specific locomotion interface used. Notwithstanding, in the second sample, significantly higher negative effects were reported in both VR conditions, indicating a possible trade-off between increased ecological validity and user comfort that needs to be considered in experimental design.

4.9 Psychometric measures of spatial abilities relation to strategy

We investigated the relationship between two widely used spatial navigation abilities tests MRT and SOT and the probability for choice in strategy. These tests are frequently used to assess spatial reasoning and orientation skills, and their scores have been correlated to navigation performance in various tasks as RAM (Astur et al. 2004; Mennenga et al. 2014), MWM (Astur et al. 2004) and others (Moffat et al. 1998), and other spatial abilities scales (Huang and Voyer 2017; Friedman et al. 2020). However, in our work, we did not observe significant correlations between strategy usage and MRT or SOT scores.

A potential explanation for this discrepancy is that most participants employed multiple strategies, place, response, and cue, during the task, which could obscure direct links between specific strategies and overall spatial ability scores. This variability highlights the complexity of strategy usage in spatial tasks, aligning with prior findings that navigation involves a dynamic interplay of cognitive processes rather than reliance on a single ability (Bohbot et al. 2007; de Condappa and Wiener 2016; Doner et al. 2023). Future work should consider how mixed strategy usage moderates the relationship between standardized cognitive tests and navigation performance.

4.10 Limitations and future directions

While our study provides valuable insights into human spatial learning in virtual environments, several limitations should be addressed in future research. The mixed results regarding the impact of VR modality on spatial learning highlight the need for more nuanced investigations of how different VR interfaces affect cognitive processes. Future studies should consider both task-specific factors and individual differences when comparing across VR modalities.

Some of the inconsistencies between the samples results suggest a limited ability to detect subtle effects as reflected in the Bayes factor analysis, implying that larger-scale studies are needed to confirm and extend our findings. Additionally, the number of three test probe trials per strategy per session may have constrained the accuracy of detecting a preferred strategy based on ET and behavioral measures. Increasing the number of probe trials could enhance the reliability of these measurements and improve both the statistical significance and effect sizes.

The integration of ET into VR headsets offers significant advantages for investigating spatial learning and strategies. Unlike EEG, which requires additional equipment and controlled laboratory settings (Lin et al., 2022; Do et al., 2021), these days ET is seamlessly integrated into modern HMDs, enabling ecologically valid studies of navigation. Furthermore, ET features provide direct insights into visual attention, which is crucial for understanding navigation strategies, as demonstrated by studies linking gaze dynamics to strategy shifts and environmental complexity (Walter et al., 2022; Zhu et al., 2022). However, the relatively minimalistic design of our task may have limited gaze behavior complexity. Therefore, designing more naturalistic and rich environments in future studies could enhance strategy differentiation based on ET data.

Our findings contribute to the ongoing discussion about the impact of VR modality on spatial cognition. Even though some studies have suggested that the neural correlates of spatial retrieval are modality-independent (Huffman and Ekstrom 2019), others have found that proprioceptive feedback can improve cognitive map accuracy (Ruddle et al. 2011). Our results suggest that the effect of VR modality on spatial learning may be task-dependent and individual and warrants further investigation.

Utilizing ET data for predictive models underscores its potential for identifying individual navigation strategies. However, the variability in gaze and behavioral patterns across trials and conditions presents challenges inherent in such endeavors. In addition to additional probe trials, and richer VR environments suggested above, future studies should

incorporate more sophisticated predictive models that account for extremely unbalanced class distribution. Likewise, combining ET data with other physiological measures (e.g., heart rate variability, and skin conductance) could assist in improving strategy prediction and deepen our understanding of the interplay between navigation behavior and physiological processes.

An additional future direction involves uncovering the neural substrates of spatial navigation strategies in the three-strategy T-maze task. Animal models have shown that spatial strategies engage distinct brain regions, with the hippocampus playing a key role in allocentric (place) strategies and the striatum supporting egocentric (response) strategies (Packard and McGaugh 1996). Subsequent human studies have provided evidence of similar neural mechanisms, demonstrating plasticity-related structural changes in London taxi drivers (Maguire et al. 2000, 2006), fMRI activations (Iaria et al. 2003) and voxel-based morphometry (VBM) analysis (Bohbot et al. 2007) in RAM adaptations, and functional connectivity in virtual MWM (Woolley et al. 2015). These findings highlight the value of translational research in bridging animal and human models of spatial navigation. Given that our study found no differences in learning effectiveness between 2D and 3D HMD VR displays after participants adapted to the interface, nor consistent differences in strategy use, employing fMRI to examine the T-maze task could offer novel insights into its neural correlates. Studying the neural mechanisms underlying the three-strategy paradigm through neuroimaging techniques would further enhance our understanding of spatial strategy selection and execution.

Our findings have potential implications for understanding and treating neurodegenerative and psychiatric conditions affecting spatial cognition. Such distinctions have been related to old age (Barnes et al. 1980; Marighetto et al. 1999; Etchamendy et al. 2012; Wiener et al. 2013) and observed in conditions like amnestic mild cognitive impairment (aMCI) (Weniger et al. 2011), Parkinson's disease (PD) (Schneider et al. 2017), obsessive-compulsive disorder (OCD) (Marsh et al. 2015), stress (Schwabe et al. 2007), Alzheimer's disease (AD) (Lithfous et al. 2013), attention deficit hyperactivity disorder (ADHD) (Robaey et al. 2016), and cocaine dependence (Tau et al. 2014). Our task's ability to disentangle the strategies involved in these studies underlines its potential to provide a sensitive tool for detecting subtle cognitive changes in these conditions. Using HMD VR-based tasks in clinical assessments offers additional advantages, as the immersive nature of VR can enhance patient engagement and motivation during evaluation procedures (Pieri et al. 2023). Importantly, by manipulating environmental features, patients could be guided toward using specific navigation strategies in our VR-based T-maze, providing a targeted approach for rehabilitating, allowing clinicians to tailor interventions to enhance particular cognitive functions or compensate for specific deficits, and foster neural plasticity.

Eventually, examining how spatial learning strategies and performance evolve over extended periods could provide insights into the potential of VR for long-term cognitive training. Future studies should explore the long-term retention of spatial knowledge acquired in different VR modalities and investigate how learning performance and the use of strategy may change over extended periods of practice.

4.11 Conclusions

This study provides novel insights into how VR modality level of immersion, locomotion interfaces, and proprioception influence spatial learning, strategy selection, and gaze behavior. Our successful translation of the classic T-maze task from (Barnes et al. 1980) that disentangles cue, place, and response strategies to human participants bridged the gap between controlled laboratory studies in animals and real-world human navigation research. We demonstrated that human navigation strategies mirror those observed in animal models while also exhibiting distinct flexibility in strategy utilization across VR conditions. The results indicated no significant differences in learning performance between HMD VR conditions (walking vs. controller). Nevertheless, the study highlighted the importance of considering modality habituation effects, particularly in 2D desktop VR, corresponding with the participants' reports of lower presence and naturalness relative to the HMD VR conditions. Our findings contribute to the ongoing debate on the role of VR immersion in spatial cognition and its related gaze behavior highlighting the importance of considering task dependency, individual differences, and habituation effects. The analysis of ET data offered insights into visual attention allocation, suggesting that physical walking may enhance attention to environmental cues. However, the prediction of navigation strategies based on ET and behavioral data yielded mixed results, likely due to individual variability in strategy usage and the relatively minimalistic task design. Overall, our translation of the T-maze task to various VR modalities contributes to a more nuanced understanding of human spatial cognition and paves the way for the development of VR-based tools for both basic research and clinical applications.

Data availability

All the data and the codes for data handling, pre-processing, analysis, and Unity task projects are available in the Open Science Framework (OSF, project page: Peer_review_link).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Declaration of generative AI in scientific writing

During the preparation of this work the authors used Preplexity and ChatGPT-4, wrapped within Consensus, for suggestions on wording and rephrasing. After using these tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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