

## Measurement of Spatial Navigation and Its Application in Cognitive Aging

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**Date:** 2019-08-15T00:00:00+00:00

### Abstract

Spatial navigation is an essential high-level cognitive function for daily life. Brain regions involved in spatial navigation, such as the hippocampus and entorhinal cortex, are susceptible to aging effects, leading to structural atrophy or functional impairment. Early studies predominantly employed experimental paradigms including animal experiments, paper-and-pencil tests, and real-world environments to investigate the characteristics of spatial navigation aging in older adults. Owing to its advantages of providing scenes similar to real-world environments, compatibility with magnetic resonance imaging scans, and enabling navigators to interact with the scenes, virtual reality technology has been increasingly applied to research on spatial navigation aging, and has further revealed the important role of medial temporal lobe brain regions such as the hippocampus in spatial navigation aging.

### Full Text

### Preamble

### Measurement of Spatial Navigation and Its Application in Cognitive Aging

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### Abstract

Spatial navigation is an essential high-level cognitive function for daily life. The brain regions involved in spatial navigation, such as the hippocampus and entorhinal cortex, are vulnerable to aging and undergo structural atrophy or

functional impairments. Early studies primarily employed animal experiments, paper-and-pencil tests, and real-world environments to investigate age-related changes in spatial navigation among older adults. Due to its advantages of providing scenes similar to real-world environments, compatibility with magnetic resonance imaging, and enabling interaction between navigators and the environment, virtual reality technology has been increasingly applied to aging research on spatial navigation, further revealing the critical role of medial temporal lobe regions like the hippocampus in age-related spatial navigation decline.

**Keywords:** spatial navigation; aging; virtual reality; hippocampus; neural mechanisms

## 1 Introduction

During healthy human aging, various cognitive functions including processing speed, memory, and executive function show age-related declines [?, ?, ?, ?, ?, ?, ?, ?, ?, ?]. Among these, getting lost is common among normal older adults and serves as an early indicator for the onset and clinical diagnosis of neurodegenerative diseases such as mild cognitive impairment and Alzheimer' s disease [?, ?, ?, ?]. Getting lost involves a crucial high-level cognitive function –spatial navigation [?, ?, ?, ?, ?, ?, ?]. Spatial navigation refers to the process of finding and remembering routes in familiar or unfamiliar environments [?, ?, ?, ?]. As a complex cognitive process, spatial navigation relies on numerous fundamental cognitive processes including vision, proprioception, and spatial representation [?, ?], and impairments in these basic abilities during aging can in turn affect spatial navigation performance [?, ?, ?, ?].

To better control for the influence of prior experience and decompose the different cognitive functions involved in spatial navigation, animal studies typically construct real-world environments in laboratories and use food or aversive stimuli to measure animals' spatial navigation performance, thereby comparing young and aged animals [?, ?, ?, ?, ?, ?, ?, ?, ?, ?]. In humans, early spatial navigation aging research primarily used paper-and-pencil tests, real-world spatial navigation tasks, or computer-based spatial memory tests to assess spatial navigation ability. With technological advances, recent studies have gradually introduced virtual reality technology, successfully measuring human spatial navigation abilities in laboratory settings by constructing virtual environments that simulate real-world navigation [?, ?, ?]. Additionally, the excellent compatibility between virtual reality technology and neuroimaging techniques enables researchers to explore structural and functional changes in brain regions related to spatial navigation during aging through non-invasive methods such as magnetic resonance imaging and electroencephalography.

Beyond measuring spatial navigation impairments in healthy aging, spatial navigation tests also demonstrate significant potential for clinical diagnosis and intervention [?, ?, ?, ?]. Alzheimer' s disease patients exhibit tau protein accumulation in the medial temporal lobe [?, ?], and abnormalities in this region,

particularly the hippocampus and entorhinal cortex, affect navigators' spatial navigation abilities [?, ?, ?]. By comparing spatial navigation performance between healthy older adults and Alzheimer' s disease patients, researchers have suggested that spatial navigation ability can serve as a cognitive predictor for Alzheimer' s disease [?, ?, ?, ?, ?, ?, ?, ?, ?, ?] and can predict conversion rates to Alzheimer' s disease over time. Healthy older adults with poorer spatial navigation performance are more likely to convert to Alzheimer' s disease within six months [?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?]. These studies demonstrate the substantial potential and application value of spatial navigation aging research.

This article summarizes measurement techniques and findings from spatial navigation aging research, covering animal studies, traditional human spatial navigation aging research, virtual reality-based spatial navigation aging research, and the neural basis of spatial navigation aging, while also proposing future research directions. We aim to encourage researchers to focus on spatial navigation aging and employ multiple technical approaches to explore the characteristics and mechanisms of age-related spatial navigation decline.

## 2 Animal Navigation Aging Research

Except for a few studies using primates [?, ?, ?, ?, ?, ?], most animal spatial navigation aging research uses mice as subjects. To simulate normal aging or Alzheimer' s disease, mouse studies typically employ mice carrying high-risk genes similar to those in Alzheimer' s disease or use brain lesion methods to pre-treat mice to mimic aging effects on medial temporal lobe regions [?, ?, ?, ?, ?, ?].

Taking the classic Morris water maze as an example, mice must locate a hidden platform in a circular pool filled with water. When mice step onto this platform, it rises to avoid the water surface [?, ?] [Figure 1: see original paper]A. This experimental paradigm has been widely adopted internationally and serves as a classic model for mouse spatial navigation experiments, including in aging research [?, ?, ?, ?, ?, ?, ?, ?, ?]. To more precisely quantify spatial navigation performance, researchers recently proposed the honeycomb maze paradigm [?, ?] [Figure 1: see original paper]B, which overcomes the limitations of the Morris water maze in terms of quantification and behavioral consistency while enabling control over choices at each decision point, yielding more detailed and comprehensive results. In this paradigm, the original circular Morris water maze is divided into multiple hexagonal platforms. At any given time, except for the platform where the mouse currently stands, at most two adjacent platforms are elevated and accessible. After the mouse chooses and moves to a new platform, the platform it left and the unchosen platforms descend and become hidden. Subsequently, two new adjacent platforms elevate to provide new spatial navigation directions [Figure 1: see original paper]C.

Researchers measure navigation efficiency by calculating the angle between each movement direction and the line connecting to the goal, assessing performance at different distances from the goal (measured by the number of hexagonal

cells along the shortest route). This paradigm ensures relatively independent decision-making at each choice point and facilitates quantification, making it an excellent model for mouse spatial navigation research [?, ?]. However, this paradigm has not yet been applied to spatial navigation aging research, representing a promising direction for future studies on both mice and humans.

The Morris water maze and honeycomb maze paradigms primarily focus on metrics such as travel distance, reaction time, and frequency of passing the hidden platform, which reflect overall spatial navigation performance but do not address specific navigation strategies. Consequently, researchers designed cross mazes and Y-mazes to measure changes in spatial navigation strategies during aging [?, ?, ?, ?, ?, ?, ?]. Research suggests that different strategies exist during spatial navigation, with the two most common being allocentric and egocentric strategies. The allocentric strategy, also known as spatial map representation, cognitive map representation, place-based strategy, or landmark-based strategy, involves navigators establishing flexible spatial map representations based on the relative spatial relationships among environmental landmarks to aid navigation [?, ?, ?, ?]. The egocentric strategy requires navigators to represent the environment relative to themselves, typically using self-motion information to encode navigation routes such as left/right turns and straight movements [?, ?, ?, ?, ?]. In cross maze studies, for instance, the maze consists of four perpendicular pathways forming a “plus” shape. Mice start in the south arm, with food or reward placed in the west arm, learning this location through repeated trials. During probe trials, mice are placed in the north arm, and their final movement serves as evidence for strategy differentiation. If mice still move to the west arm, they are considered to have correctly located it using the relative spatial relationships of external landmarks (allocentric strategy). If they move to the east arm, they are considered to have used body-turn information such as “turn right” (egocentric strategy) [?, ?]. These spatial navigation strategy studies have found that aged mice preferentially adopt egocentric strategies and show impairments in using allocentric strategies, providing foundational evidence for human spatial navigation aging research [?, ?, ?, ?, ?].

Animal-based spatial navigation aging research offers unique advantages and tremendous potential, enabling direct recording of neurophysiological signals to provide direct evidence for spatial navigation aging, including behavioral manifestations [?, ?], changes in neurotransmitters during aging [?, ?], and correlations between EEG oscillation frequencies and behavior [?, ?]. The Nobel Prize-winning discovery of grid cells was also based on mouse spatial navigation research, providing insights and directions for human spatial navigation aging studies [?, ?, ?, ?].

### 3 Traditional Human Spatial Navigation Aging Research

Early spatial navigation aging research in humans typically used paper-and-pencil tests to assess spatial navigation ability, including the Wechsler Block Design Test [?, ?, ?, ?, ?, ?], Money Road-Map Test [?, ?, ?, ?], and Mental

Rotation Test [?, ?, ?, ?]. However, these paper-and-pencil tests differ substantially from real-world spatial navigation [?, ?], and previous research has found that their results only partially reflect actual spatial navigation performance, lacking sensitivity [?, ?].

Consequently, some researchers turned to real-world environments for spatial navigation aging studies. In these studies, researchers selected specific real-world environments or routes, including hospitals [?, ?], indoor spaces [?, ?, ?, ?, ?, ?], streets [?, ?], and parks [?, ?, ?, ?, ?]. Researchers typically guided participants through these environments before using paper-and-pencil tests for recall measurement to evaluate spatial navigation ability. Compared to paper-and-pencil tests, these real-world spatial navigation aging studies allow participants to actually navigate in physical environments, yielding results that better capture genuine spatial navigation ability rather than just specific aspects such as spatial memory or visuospatial processing [?, ?]. These real-world spatial navigation aging studies provide greater practical value, such as informing community design to reduce older adults' wayfinding difficulties based on their spatial navigation characteristics [?, ?]. Despite these advantages, real-world spatial navigation aging research has many limitations, including complexity, time and labor intensity, and difficulty in controlling for numerous extraneous variables compared to laboratory settings.

With advances in computer technology, increasing numbers of researchers have begun using computer-presented stimuli. These studies focus primarily on basic spatial perception, examining age-related changes in spatial processing under passive viewing of pure visual flow input [?, ?, ?, ?, ?, ?, ?, ?, ?, ?]. In these experiments, participants simply receive simple visual stimuli. In the triangle completion task, for example, participants sit before a computer screen, passively watch a video, and at the end make judgments about spatial information such as distance and rotation angle. Different task types are illustrated in [Figure 2: see original paper] [?, ?, ?, ?]. When reporting rotation angles in the video, older adults tend to overestimate small angles and underestimate large angles [?, ?]. However, no age differences exist in rotation angle estimation, whereas older adults show significantly greater error than younger adults in distance estimation [?, ?].

Additionally, researchers have used other paradigms, including static picture presentation, to measure age-related changes in cognitive functions related to spatial navigation, reporting impairments in allocentric reference frame encoding with relatively preserved egocentric reference frames [?, ?, ?, ?, ?] and slowed memory speed for spatial representations [?, ?, ?, ?] in older adults. These computer-based spatial navigation aging studies decompose spatial navigation ability into relatively basic cognitive functions for measurement and allow good control of extraneous variables. However, they also have limitations, as the measured content still cannot truly reflect spatial navigation ability but rather represents basic cognitive processes related to spatial navigation, such as spatial representation and path integration.

## 4 Virtual Reality-Based Spatial Navigation Aging Research

In recent years, virtual reality technology has been increasingly used to measure age-related changes in human spatial navigation ability. Virtual reality technology refers to presenting visual images and non-visual multimedia stimuli to provide interactive scenes that immerse users in a virtual environment [?, ?, ?, ?, ?]. Compared to real-world spatial navigation aging research, virtual reality technology is relatively time- and labor-efficient while enabling strict experimental control and reducing extraneous variables [?, ?]. Virtual reality spatial navigation experiments differ from computer-based spatial navigation tasks in two main aspects: the virtual environment and interactivity. First, virtual reality spatial navigation tasks use scenes similar to real-world environments (using photographs or constructed virtual environments) rather than simple visual flow or visual cues. Second, navigators interact with the virtual environment through active manipulation or passive viewing, resulting in actual displacement within the virtual space. These features distinguish virtual reality spatial navigation experiments from traditional spatial cognitive tasks, providing researchers with optimized methods for measuring spatial navigation aging.

Some researchers have compared real-world and virtual reality spatial navigation performance by constructing virtual environments identical to real-world settings and measuring various spatial navigation outcomes including route learning, landmark recall, and photograph recall. Results show strong correlations between overall spatial navigation performance in real and virtual environments across young adults, older adults, mild cognitive impairment patients, and early Alzheimer' s disease patients ( $r=.73$ ), demonstrating the validity of virtual reality technology in spatial navigation aging research [?, ?, ?, ?].

The combination of virtual reality technology and traditional mouse spatial navigation paradigms has been successfully applied to human participants, including radial arm mazes (eight-arm or twelve-arm) [?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?, ?], cross mazes [?, ?, ?, ?], star mazes [?, ?, ?, ?, ?, ?, ?], and Morris water mazes [?, ?, ?, ?, ?, ?]. These virtual reality paradigms can be further categorized based on research purposes. The Morris water maze focuses on spatial navigation performance metrics including navigation speed and error rates [?, ?, ?, ?]. Similar to animal research findings, these virtual reality spatial navigation studies have found impairments in older adults on these measures, such as slower navigation speed and increased error rates [?, ?, ?, ?]. Building on the Morris water maze, researchers designed the circular arena paradigm, which resembles the Morris water maze in requiring navigators to remember object locations in the environment and move toward them, using metrics such as distance error, travel distance, and reaction time to assess performance [?, ?, ?, ?, ?, ?, ?, ?, ?, ?]. Using this paradigm combined with magnetic resonance imaging, researchers first discovered grid-cell-like representations in humans. They found that healthy adults carrying Alzheimer' s disease high-risk genes already showed decreased activation of grid-cell-like representations [?, ?], and healthy older adults sim-

ilarly exhibited decreased activation levels, potentially explaining mechanisms underlying spatial navigation performance impairments [?, ?].

In contrast, cross maze and radial arm maze paradigms primarily focus on spatial navigation strategy selection and usage. Virtual reality spatial navigation studies using these paradigms have found that older adults show impairments in strategy selection and switching [?, ?, ?, ?]. Additionally, human virtual reality spatial navigation aging research frequently employs star maze paradigms [?, ?, ?]. These studies typically divide tasks into learning trials and probe trials. During repeated learning trials, participants start from the same location and navigate to a fixed goal. In the final probe trial, the starting location is changed without participants' knowledge, and strategy differentiation is based on their responses, as illustrated in [Figure 3: see original paper] [?, ?, ?, ?, ?, ?, ?].

Research has found that young adults use multiple strategies during spatial navigation, including route-based strategies, stimulus-response association strategies, and trial-and-error strategies [?, ?, ?], while most studies have focused on allocentric and egocentric strategies [?, ?, ?, ?]. Previous research has found that only allocentric strategies are impaired during aging, while egocentric strategies remain intact [?, ?, ?, ?, ?, ?, ?]. Since egocentric strategies resemble stimulus-response learning [?, ?], using egocentric strategies requires remembering body turns when encountering specific environmental landmarks—a series of stimulus-response associations similar to episodic memory that includes both temporal and spatial information [?, ?]. In contrast, using allocentric strategies for spatial navigation requires more cognitive functions, including encoding spatial scenes to form cognitive maps, extracting allocentric representations, and route planning [?, ?, ?, ?, ?, ?, ?, ?]. These processes may involve activation of the frontoparietal control network, suggesting that allocentric navigation requires more cognitive resources than egocentric strategies [?, ?, ?, ?, ?], which may explain why older adults show impairments in allocentric strategies. Furthermore, according to the retrogenesis theory, abilities acquired earlier in development are more enduring and less susceptible to aging effects, while later-acquired abilities are more vulnerable to age-related decline [?, ?]. Studies have reported that 5-year-old children already possess egocentric strategies, which are considered relatively basic representations [?, ?]. In contrast, allocentric strategies are acquired later, with 10-year-old children only then able to use them correctly and efficiently [?, ?]. Therefore, allocentric strategies are considered more vulnerable to aging and will be impaired before egocentric strategies [?, ?]. Nevertheless, successful spatial navigation requires flexible strategy selection and switching according to environmental demands rather than relying on a specific strategy [?, ?, ?]. Virtual reality spatial navigation studies have found that young adults simultaneously use both egocentric and allocentric strategies [?, ?], but older adults show impairments in selecting appropriate strategies, often choosing unsuitable strategies during navigation [?, ?, ?]. The question of what constitutes an appropriate strategy varies with environment and task demands [?, ?, ?, ?, ?, ?, ?, ?]. For example, research has found that egocentric strategies are more effective when navigating along fixed routes or in familiar

environments, reducing decision time and avoiding wrong paths, whereas allocentric strategies (spatial cognitive maps) are more effective when navigating in novel environments or planning routes [?, ?]. Currently, few studies have examined age-related changes in strategy selection ability, with existing research reporting that older adults show impairments in switching from egocentric to allocentric strategies [?, ?, ?]. Therefore, although some studies report that older adults' egocentric strategies remain relatively intact, if older adults cannot select appropriate strategies, their spatial navigation performance will still be impaired, suggesting that spatial navigation aging interventions could begin with strategy selection.

Additionally, based on participants' familiarity with experimental materials, spatial navigation environments can be divided into familiar and novel environments. The former can investigate interference from existing experience on similar scene learning, while the latter can exclude prior experience effects to measure age-related changes in spatial navigation learning [?, ?, ?, ?, ?, ?]. These differences in spatial navigation paradigms illustrate that researchers must select appropriate paradigms and adapt them according to experimental purposes and hypotheses to measure variables of interest. Particularly in spatial navigation aging research, when adapting paradigms, researchers must consider older adults' capabilities and appropriately reduce task difficulty and simplify experimental operations. For example, the Morris water maze paradigm, as a classic spatial navigation model, has been extensively applied to human participants, including virtual reality versions [?, ?] and real-world versions [?, ?]. However, these versions are adaptations of the original mouse paradigm, resulting in many differences in environmental layout and spatial size. Furthermore, to measure interactions between spatial navigation strategies and performance, some researchers have adapted the Morris water maze into new circular arena paradigms [?, ?], which can measure not only the original spatial navigation performance metrics but also strategy changes and spatial reference frame preferences during aging [?, ?, ?]. Moreover, considering older adults' unfamiliarity with computer controls and impaired fine motor movements, virtual reality spatial navigation aging research can replace active manipulation with passive viewing (or reduce task button-press difficulty), allowing older adults to passively watch displacement in virtual environments and make button responses afterward while recording brain activity. This approach prevents spatial navigation performance impairments caused by allocating excessive attentional resources to fine motor movements. Therefore, in virtual reality spatial navigation aging research, it is crucial to select appropriate spatial navigation paradigms based on experimental purposes and modify them as needed. For instance, some researchers have used custom-designed virtual environments and tasks to measure age-related changes in spatial navigation ability. One study created a rectangular room-style virtual environment to compare spatial navigation performance between moving and fixed viewpoint conditions [Figure 4: see original paper]A, finding that older adults showed impaired spatial representation memory under fixed viewpoints [?, ?, ?, ?, ?]. Another study combined virtual reality environ-

ments with wheelchairs to design a novel spatial navigation task [Figure 4: see original paper]B, where navigators pushed wheelchairs through a three-story virtual building to find specific rooms. The study found that various error metrics correlated significantly with age and general cognitive level, with older adults showing more navigation errors than younger adults [?, ?, ?, ?, ?].

The combination of virtual reality technology and spatial navigation paradigms is not limited to theoretical research but also demonstrates substantial application value in clinical diagnosis, aging intervention, and rehabilitation [?, ?, ?, ?, ?]. Studies have found that virtual reality spatial navigation performance can distinguish Alzheimer' s disease patients from healthy older adults and other patient groups [?, ?, ?, ?]. For example, researchers used the virtual reality star maze paradigm to measure spatial navigation performance in healthy young adults, healthy older adults, frontotemporal dementia patients, mild cognitive impairment patients, and Alzheimer' s disease patients. The study found that spatial navigation performance was more effective than traditional neurocognitive tests in distinguishing Alzheimer' s disease patients from healthy older adults and frontotemporal dementia patients, and more accurately predicted conversion rates from mild cognitive impairment to Alzheimer' s disease after six months [?, ?]. In aging intervention, studies have also found that virtual reality spatial navigation training can improve spatial navigation performance and even slow gray matter volume decline [?, ?, ?]. For instance, one study used a treadmill combined with virtual reality spatial navigation tasks to conduct a four-month intervention with older adults. In this study, a virtual environment was projected on a screen in front of the treadmill, with participants' movements on the treadmill directly reflected in the virtual environment. During training, participants had to learn and locate objects scattered throughout the virtual environment. By comparing structural magnetic resonance imaging data before and after training, researchers found that virtual reality spatial navigation tasks could slow hippocampal volume decline [?, ?]. These studies demonstrate the important practical value of virtual reality spatial navigation tasks.

## 5 Neural Mechanisms of Spatial Navigation Aging

Compared to real-world spatial navigation aging research, virtual reality technology presents stimuli through computer screens, simulating real spatial navigation processes through visual input without requiring extensive body movement, allowing researchers to combine various neuroimaging techniques to deeply explore brain activity during spatial navigation.

Animal spatial navigation aging research has yielded interesting findings regarding neural mechanisms, providing insights for human studies. By adapting animal research paradigms and combining them with magnetic resonance imaging, researchers have discovered similar results in humans [?, ?]. Spatial navigation, as a complex cognitive activity, involves numerous brain regions including the hippocampus, parahippocampal gyrus, striatum, entorhinal cortex, medial temporal lobe, prefrontal cortex, posterior parietal cortex, and retrosplenial cortex

[?, ?, ?, ?]. These regions provide different types of support for spatial navigation and show distinct changes during aging.

Traditionally, the hippocampus has been considered responsible for episodic memory encoding and storage. With the discovery of place cells, researchers found that the hippocampus is also involved in allocentric spatial navigation, responsible for forming cognitive map representations to facilitate spatial navigation [?, ?, ?]. As a central hub for spatial navigation, the hippocampus receives projections from primary sensory cortices and the entorhinal cortex, and outputs processed information back to numerous spatial navigation-related regions including the entorhinal cortex, striatum, and parahippocampal gyrus [?, ?, ?]. The hippocampus is vulnerable to aging, with studies reporting volume atrophy and functional impairments during normal aging [?, ?, ?]. These impairments affect allocentric strategy use, including cognitive map formation and memory retrieval [?, ?]. Additionally, the hippocampus may be responsible for spatial vector computation, providing preliminary processing for higher-level route planning [?, ?], with information generated in the hippocampus further output to the prefrontal cortex to inform strategy selection [?, ?, ?]. Therefore, aging in this region severely impacts older adults' spatial navigation ability.

Most previous studies have analyzed the hippocampus as a whole, ignoring its subregions. With advances in high-resolution magnetic resonance imaging, increasing numbers of studies have begun subdividing the hippocampus, revealing structural and functional differences across subregions [?, ?, ?] and differential effects of aging and age-related diseases on these regions [?, ?, ?]. Taking the dentate gyrus (DG) and CA3 region (cornu Ammonis 3) as examples, the dentate gyrus is responsible for pattern separation—for similar input stimuli, this region can correctly distinguish differences between stimuli, amplify their distinctiveness, and encode them as separate representation patterns [?, ?]. However, this region is vulnerable to aging-related atrophy [?, ?, ?]. Due to damage in this region, older adults cannot distinguish similar stimuli and scenes [?, ?]. In contrast, the hippocampal CA3 region is responsible for pattern completion. Except for minor projections to the CA1 region, over 95% of projections return to the CA3 region itself via recurrent collaterals. These fibers function to repeatedly complete incomplete input stimuli through self-connections, forming complete patterns [?, ?]. This region is relatively preserved during aging and is less susceptible to structural atrophy or functional impairment [?, ?, ?, ?]. In studies examining hippocampal subregion aging, most have measured changes in these regions through similar memory assessments, but few have measured how age-related changes in these regions manifest in spatial navigation ability, representing a major direction for future spatial navigation aging research.

Since the discovery of grid cells, the entorhinal cortex has attracted substantial research attention [?, ?]. Most studies have used mouse experiments to record grid cell firing patterns in the entorhinal cortex during real-world spatial navigation [?, ?]. With advances in virtual reality technology, researchers using task-based functional magnetic resonance imaging have discovered grid-cell-like

representation activation in human entorhinal cortex [?, ?, ?, ?], supporting the notion that grid cell spatial firing patterns in the entorhinal cortex are also important components of human spatial navigation. However, the entorhinal cortex is also vulnerable to aging, with age-related atrophy and tau protein accumulation in this region often associated with Alzheimer's disease [?, ?]. Another virtual reality study of healthy older adults found that even healthy older adults showed decreased grid-cell-like activation during object-location tasks, and this decrease correlated with path integration performance [?, ?]. These findings on entorhinal cortex aging provide research directions for healthy aging, suggesting that spatial navigation aging research results can offer early predictive diagnostic indicators for aging-related diseases [?, ?].

Although the frontal lobe is not directly responsible for spatial navigation processing, numerous studies have found that it participates in functions such as strategy selection, route planning, and shortcut selection during spatial navigation [?, ?, ?, ?, ?]. Colombo et al. (2017) reported that older adults show significant impairments in switching from egocentric to allocentric strategies, possibly regulated by the prefrontal cortex. The prefrontal cortex receives information input from the hippocampus, makes strategy judgments, and projects these judgments back to the hippocampus. Damage to the prefrontal cortex during this process affects strategy judgment, leading older adults to make incorrect strategy choices [?, ?, ?]. Additionally, some studies suggest that the ventromedial prefrontal cortex and orbitofrontal cortex are primarily responsible for allocentric spatial navigation, while the dorsomedial prefrontal cortex is primarily responsible for egocentric spatial navigation [?, ?].

## 6 Summary and Outlook

During healthy aging and aging-related neurodegenerative diseases in older adults, spatial navigation ability is highly susceptible to impairment [?, ?]. Since spatial navigation ability is closely related to daily life, its impairment restricts older adults' activity range and reduces their quality of life. To better intervene in older adults' spatial navigation ability, it is necessary to explore the mechanisms underlying spatial navigation aging more deeply [?, ?]. Previous studies have reported impairments in older adults' spatial navigation strategy selection or in executing specific strategies but have paid less attention to their interaction. Some research suggests that allocentric strategies are impaired first, forcing older adults to adopt extra-hippocampal strategies (such as egocentric strategies) [?, ?, ?, ?, ?, ?, ?, ?, ?]. However, other studies indicate that older adults' primary impairment is the ability to flexibly select appropriate strategies based on task and environmental demands. Older adults have difficulty quickly and correctly switching between multiple strategies and show a preference for egocentric strategies [?, ?, ?]. When older adults navigate in environments unsuitable for egocentric strategies, spatial navigation efficiency is lower, even if they can learn both strategies simultaneously [?, ?, ?, ?, ?]. Therefore, it remains unclear whether strategy impairments affect navigation performance or

vice versa, requiring further verification. Notably, only one study has used two separate tasks to measure aging effects on both aspects, finding that older adults have difficulty switching from egocentric to allocentric strategies and that this impairment correlates with shortcut selection [?, ?]. Therefore, using navigation tasks to simultaneously measure age-related changes in both spatial navigation performance and strategies and exploring their interactions will be an important future direction in spatial navigation aging research.

Early animal spatial navigation aging experiments provided irreplaceable evidence of neural activity, particularly at the cellular level. Compared to human studies, these studies' greatest advantage lies in the ability to strictly control subjects' age, genetics, and brain lesions while measuring neural activity at a more microscopic level. Although these conclusions cannot be directly generalized to humans, they provide important insights for human neural mechanism research. For example, early researchers discovered special firing patterns of grid cells in the mouse entorhinal cortex, but for healthy human participants, researchers cannot directly record firing patterns of individual cells. As mentioned previously, to verify the existence of grid cells in human entorhinal cortex, researchers combined virtual reality with functional magnetic resonance imaging and discovered grid-cell-like activation representations in the entorhinal cortex, which showed age-related decline [?, ?, ?]. Similarly, other animal studies have provided many insights for measuring human spatial navigation aging, and future human spatial navigation aging research can build on these cutting-edge animal findings to verify their generalizability to human participants.

Human spatial navigation aging research has evolved from paper-and-pencil tests, real-world spatial navigation experiments, and simple visual stimulation studies toward virtual reality spatial navigation research. Unlike the first three approaches, virtual reality technology allows researchers to construct virtual environments according to experimental purposes, enabling strict control of extraneous variables [?, ?]. This technology's excellent compatibility with various in vivo brain imaging techniques facilitates revealing the neural mechanisms of human spatial navigation aging [?, ?, ?]. Additionally, virtual reality training can improve spatial navigation ability, providing technical means for spatial navigation aging intervention. The advantages demonstrated by virtual reality technology prove its tremendous potential in spatial navigation aging research, and future researchers should adopt virtual reality technology to measure age-related changes in spatial navigation ability and use it for intervention.

As a high-level cognitive function, spatial navigation is complex. Although different brain regions provide different types of support for spatial navigation, the connections between these regions during spatial navigation remain unclear and await future verification and the establishment of corresponding spatial navigation aging models. For example, existing research has established a simple spatial navigation cognitive model: primary sensory input projects simultaneously to the hippocampus and striatum for preliminary spatial information processing, with both outputs projecting to the prefrontal cortex, which

ultimately makes decisions and selects appropriate spatial navigation strategies [?, ?, ?]. Whether this model applies to older adults remains unclear due to limited evidence and requires further exploration. Taking prefrontal-hippocampal functional connectivity as an example, hormone levels in the prefrontal cortex are prone to abnormalities during mouse aging [?, ?, ?, ?, ?], which may affect older adults' strategy selection. Studies have found that patients with mild cognitive impairment show lower prefrontal-hippocampal functional connectivity than healthy older adults during both recall tasks and resting-state scans [?, ?, ?]. Future spatial navigation aging research should combine virtual reality with neuroimaging techniques to further explore the primary brain regions responsible for age-related declines in spatial navigation ability and investigate these changes at the levels of brain structure, functional activation, functional connectivity, and functional networks.

Moreover, since brain regions related to spatial navigation are vulnerable to aging-related structural atrophy and functional impairments, research on older adults' spatial navigation ability will help reveal brain aging mechanisms and provide new insights for diagnosing and intervening in both normal aging and neurodegenerative diseases.

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