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Reaching the Goal: Superior Navigators in Late Adulthood Provide a Novel Perspective into Successful Cognitive Aging

Ruojing Zhou,[a] Tuğçe Belge,[a] Thomas Wolbers[a,b]

[a]*Aging, Cognition and Technology Lab, German Center for Neurodegenerative Diseases*
[b]*Center for Behavioral Brain Sciences, Magdeburg*

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Abstract

Normal aging is typically associated with declines in navigation and spatial memory abilities. However, increased interindividual variability in performance across various navigation/spatial memory tasks is also evident with advancing age. In this review paper, we shed the spotlight on those older individuals who exhibit exceptional, sometimes even youth-like navigational/spatial memory abilities. Importantly, we (1) showcase observations from existing studies that demonstrate superior navigation/spatial memory performance in late adulthood, (2) explore possible cognitive correlates and neurophysiological mechanisms underlying these preserved spatial abilities, and (3) discuss the potential link between the superior navigators in late adulthood and SuperAgers (older adults with superior

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Correspondence should be sent to Ruojing Zhou, German Center for Neurodegenerative Diseases, Aging & Cognition Research Group, Leipziger Str. 44, 39120 Magdeburg, Germany. E-mail: Ruojing.Zhou@dzne.de Thomas Wolbers, Center for Behavioral Brain Sciences, Universitätsplatz 2, 39106 Magdeburg, Germany. E-mail: Thomas.Wolbers@dzne.de

episodic memory). In the closing section, given the lack of studies that directly focus on this subpopulation, we highlight several important directions that future studies could look into to better understand the cognitive characteristics of older superior navigators and the factors enabling such successful cognitive aging.

Keywords: Spatial navigation; Cognitive aging; Hippocampus; Episodic memory; Superaging

Aging has a significant impact on a range of cognitive abilities, including spatial learning and navigation. While old age is typically associated with declining spatial memory/navigational abilities and altered neural mechanisms supporting navigation behavior, some individuals retain their ability to form highly accurate spatial memories and to navigate successfully their surroundings, comparable to their younger counterparts, even in advanced age (Fig. 1). Understanding how such maintenance of spatial abilities is achieved is of particular interest because it provides a unique window into understanding how the aging brain copes with neurodegenerative changes and adapts accordingly to maintain optimal functions.

In the following sections, we first review behavioral evidence that demonstrates superior performances in some older individuals across different navigational and spatial memory tasks. Since there is yet no study, to the best of our knowledge, that has explicitly investigated good navigators in old age and the cognitive/physiological characteristics contributing to their exceptional performance, we focus here on human behavioral studies where interindividual variability is observed (i.e., older individuals whose task performance was comparable to those of the healthy young controls). Furthermore, we discuss potential cognitive correlates, including both navigation-specific and domain-independent cognitive abilities, that could contribute to superior spatial memory and navigational performance in some older adults.

Second, we highlight the neurophysiological factors that could support successful maintenance of superior navigation abilities and spatial memory in advanced age. Given what is known about the neural mechanisms underlying spatial navigation and how aging impacts the relevant systems, we speculate what contributing factors/mechanisms would lead to successful cognitive aging in the context of navigation abilities.

Third, we briefly explore possible connections between SuperAgers and superior navigators in old age. SuperAgers are defined as people in advanced age (above 80) whose episodic memory performance is comparable to that of cohorts 2–3 decades younger (Harrison, Weintraub, Mesulam, & Rogalski, 2012; Rogalski et al., 2013). Aside from youthful episodic memory capacity, SuperAgers perform within one standard deviation of the average range for their age in measures of other cognitive abilities, such as executive functioning and semantic retrieval. Episodic memory is one of the hallmarks of hippocampal functions, and the parallels between this process and spatial navigation/memory have been discussed in several review papers (Buzsáki & Moser, 2013, Burgess, Maguire, & O'Keefe, 2002; Rueckemann, Sosa, Giocomo, & Buffalo, 2021; Sugar & Moser, 2019). It is thus important to examine navigational and spatial memory abilities in SuperAgers as well as episodic memory in older superior navigators. Understanding the link between the two cohorts will lend us critical

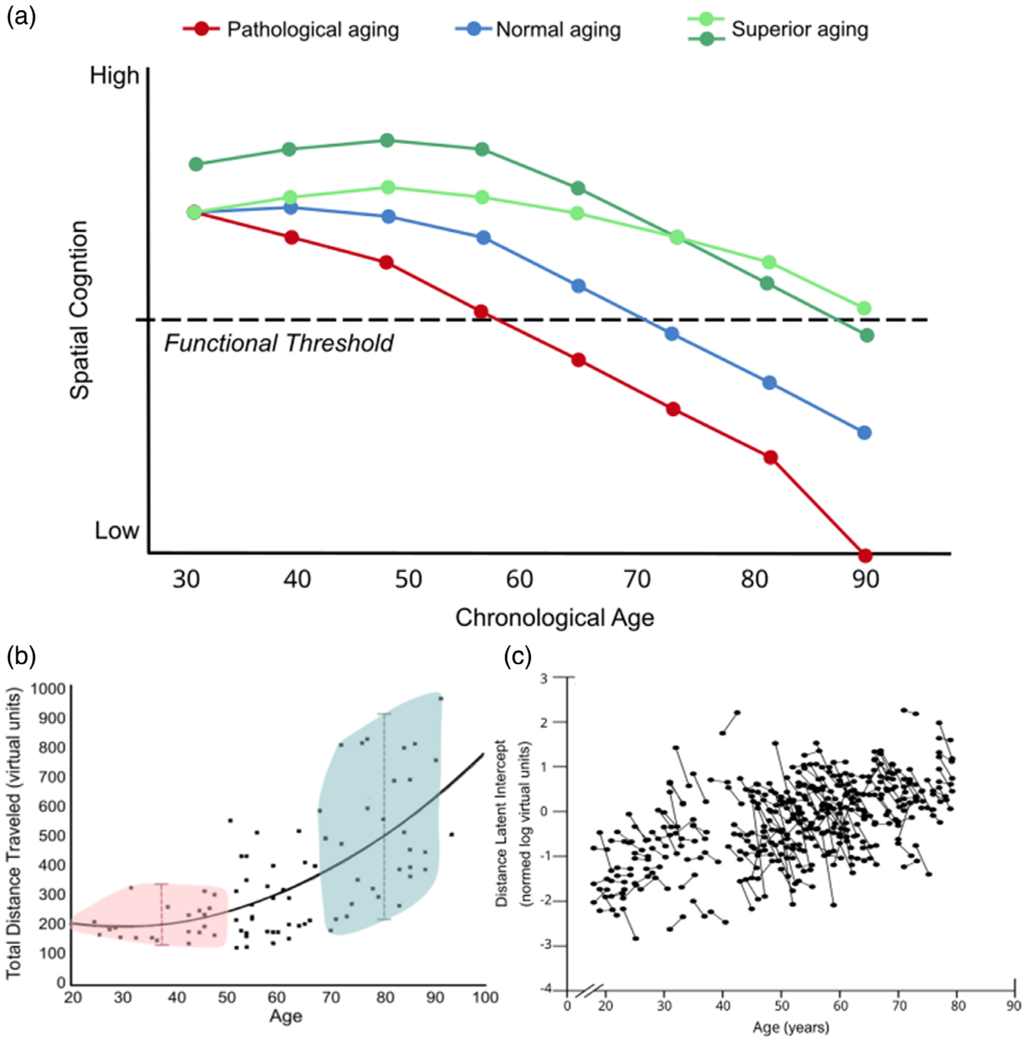

Fig. 1. Individual variability in the development of spatial memory and navigational abilities across the lifespan. (a) Schematic illustration of hypothetical developmental trajectories through early, middle, and late adulthood. While pathological and normal aging are associated with a decrease in spatial cognition, successful or superior aging is marked by much slower or even a lack of degradation in performance. Such interindividual differences in the rate of change in spatial cognition might lead to greater performance variability in late adulthood. (b) Scatterplot depicting the length of search paths used by participants to locate a hidden target in a virtual Morris water maze (vMWM) task, with shorter distance indicating better performance. Beyond a general increase in travel distance across age groups, performance variability is visibly much greater in the older age groups (70–90) than in the younger age groups (20–50). Adapted from Moffat and Resnick (2002). However, it should be noted that increased individual differences in performance could also be due to task difficulty in that the performance of the younger cohorts may have reached ceiling level, thereby reducing variability. (c) Individual change trajectories between baseline and follow-up visits with 2 years apart for search path length in a vMWM task. Greater, more positive values indicate worse performance. Heterogeneity in the rate of change can be observed. Adapted from Daugherty and Raz (2017).

insight into successful aging as well as a deeper knowledge of the computations underlying the navigation/memory circuits.

In the final section, we provide an outlook on important directions for future research. We believe that understanding how the brain adaptively copes with aging could help promote successful aging in a broader population.

1. Which cognitive abilities contribute to superior navigation/spatial memory performance in old age?

1.1. *Preserved* spatial abilities *leading to successful navigation/spatial memory performance in late adulthood*

The ability to find and remember one's way in complex environments is multifaceted and includes multiple, parallel spatial processes. At the very basic form, path integration (PI) is a critical skill to keep us oriented even when minimal environmental cues are available (Fig. 2a). PI refers to the capacity to continuously track changes in one's position and orientation by integrating body-based self-motion cues (vestibular and proprioceptive) as well as visual optic flow information. In addition, one can also acquire navigation-relevant information from external environmental features. Landmarks, distinct permanent objects in our surroundings (e.g., a city hall), are one type of important navigational cues because they are useful for determining one's heading and position during navigation (Knierim & Hamilton, 2011). Moreover, associations between actions and local landmarks can facilitate route learning, the acquisition of the sequence of turning directions at decision points.

Spatial knowledge can be organized either in an egocentric or in an allocentric reference frame (Fig. 2b). On the one hand, locations of interest can be specified relative to oneself (e.g., left panel in Fig. 2b); when one moves, the spatial vector between oneself and the target also changes. On the other hand, locations can also be specified relative to external cues irrespective of the location and orientation of the navigator (e.g., right panel in Fig. 2b). Such allocentric, relational knowledge among different points of interest constitutes a cognitive map representation of our surroundings, which guides flexible, goal-directed behaviors across time and space.

With all these building blocks of spatial navigation in mind, we review evidence of superior performance in subsets of older adults across the various spatial abilities. By looking into what aspects of and how the spatial processes could be preserved in advanced age, we will establish a novel perspective on understanding mechanisms of successful cognitive aging.

1.1.1. Path integration

A fundamental type of navigation strategy, PI, is essential for updating one's internal location representation in relation to the starting point of one's journey. More importantly, PI supports a cognitive-map representation because the process allows us to associate environmental cues with internal position estimates (Wang, 2016). While PI performance generally declines with age (Adamo, Briceño, Sindone, Alexander, & Moffat, 2012; Harris & Wolbers,

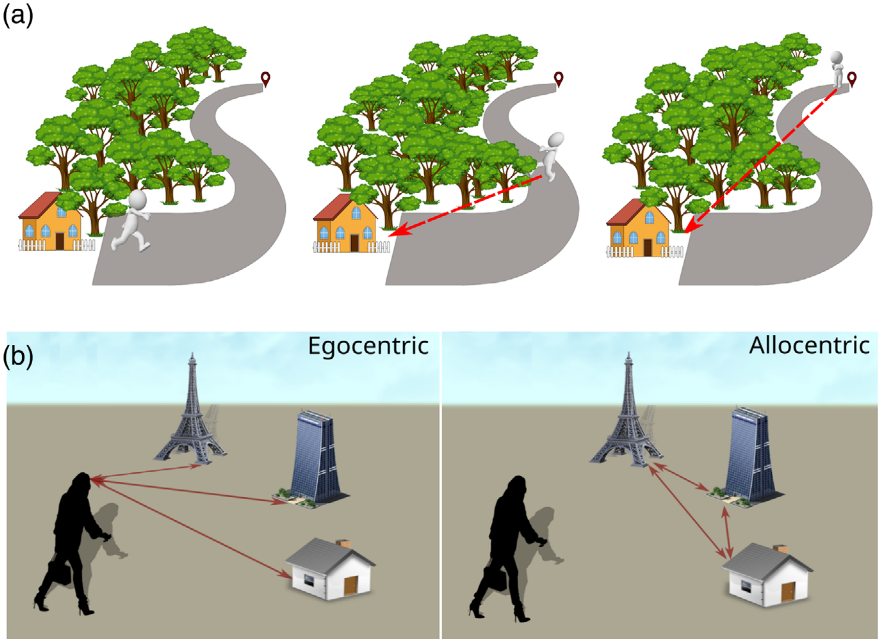

Fig. 2. Schematic illustrations of a common path integration task and the different reference frames in spatial coding. (a) A path integration task that one frequently encounters in daily life. The navigator moves from a start location (e.g., home marked as the house) to the destination. The position of the navigator along the trajectory can be estimated from proprioceptive, vestibular, and visual optical flow information generated from self-motion. Thus, a homing vector (depicted as the red arrow in the middle and right panels) pointing toward the start from the navigator's current location can be computed and continuously updated, ensuring that the navigator can keep track of where they are relative to the start location. (b) The left panel illustrates an example of the egocentric reference frame where target locations are encoded relative to the observer; the right panel illustrates the allocentric reference frame where locations of interest are encoded relative to some external reference point, for example, the Eiffel tower.

2012; Stangl et al., 2018), behavioral evidence points to preserved performance in some older individuals and under some task conditions.

One classic paradigm to study PI is the triangle completion task, during which participants are asked to indicate the starting point after traversing through the first two legs of a triangular pathway. Older adults show impaired performance when movement information during the outbound paths is restricted to single sensory sources (vestibular only [Allen, Kirasic, Rashotte, & Haun, 2004] or visual optical flow only [Adamo et al., 2012]). However, they are able to improve localization accuracy when multiple sources of idiothetic information are available (e.g., walking [Adamo et al., 2012; Allen et al., 2004]). Furthermore, older participants who were more precise in self-motion perception (the ability to estimate one's moving speed and direction) also demonstrated better PI performance in a real-waking PI task (Stangl, Kanitscheider, Riemer, Fiete, & Wolbers, 2020). Together, these findings suggest that maintaining a precise self-motion estimation might be critical for superior PI performance in old age.

Modeling work has characterized multiple error sources contributing to inaccurate location estimates during PI (Stangl et al., 2020). These sources include noise in self-motion inputs, information decay in the path integrator itself (suboptimal integration of self-motion estimates over time), and reporting noise in the conversion of the location estimates into behavioral readouts. In particular, imperfect self-motion estimation appears to be one major error source and is further magnified in aging (Stangl et al., 2020). Importantly, self-motion perception itself is complex and multimodal in that multimodal sensory signals are integrated to form a unified self-motion estimate (Campbell & Giocomo, 2018).

With regard to age-related changes, older adults might be more affected by noisy sensory inputs in that aging diminishes the reliability of the visual and vestibular information generated by self-motion. To counteract such loss in "unisensory" perception, heightened multisensory integration is observed in older adults both in self-motion perception and other perceptual domains (Freiherr, Lundström, Habel, & Reetz, 2013; Lich & Bremmer, 2014; Ramkhalawansingh, Keshavarz, Haycock, Shahab, & Campos, 2017). Thus, superior PI with self-motion cues in some older adults might be a result of either more accurate perception of "unisensory" inputs or enhanced multisensory integration in response to age-related declines in early perceptual systems. Future research should examine if and how older superior performers benefit from these two stages of self-motion perception. For instance, older superior performers could be tested in PI tasks with restricted (e.g., wheelchair transportation or visual optical flow only) as well as "full" sensory information (walking) available. If older superior performers benefit from preserved "unisensory" perception of self-motion, their PI performance would be comparable across the different transportation conditions, regardless of the level of availability in idiothetic information during outbound paths.

Because self-motion cues are prone to error accumulation, self-location estimates become noisier and less accurate as the length of an outbound path increases. Proximal visual landmarks can be used to reduce such errors. Specifically, location estimates based on visual landmarks can be integrated with those based on self-motion cues to obtain a better estimate. Optimal cue integration is, therefore, beneficial in reducing uncertainty/noise of location estimates based on single cues and improving localization accuracy. Older adults have been shown to improve their localization performance in a real-walking homing task when both self-motion and visual-landmark cues are available, in comparison to conditions when only one type of cues is present (Bates & Wolbers, 2014; Fig. 3a). Moreover, some individuals even achieved high-level performance comparable to the group mean of younger participants (Fig. 3b). Correspondingly, older participants demonstrated a significant reduction in response variance in the double-cue condition compared to the single-cue conditions, suggesting the benefit of cue integration (although their cue-integration was suboptimal at the group level).

One possibility of the better performance in some older participants in the double-cue condition could be due to statistically optimal cue integration (although this was not shown in Bates & Wolbers, 2014). Future studies should, therefore, examine if optimal cue integration contributes to exceptional PI in older adults when both self-motion and landmark cues are available. Such knowledge might also be informative in helping normal agers improve

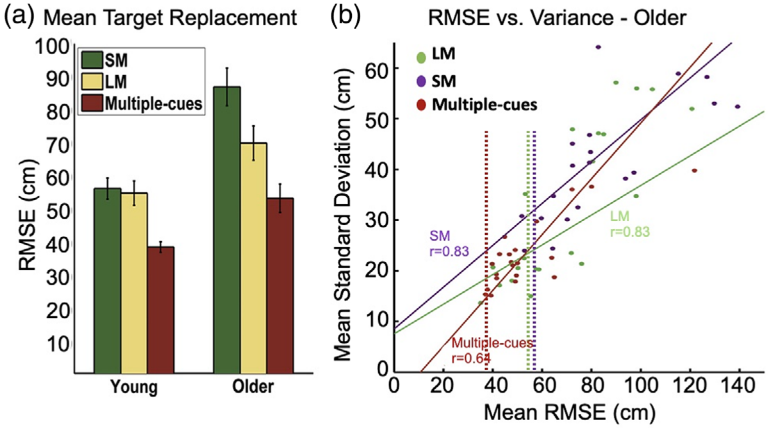

Fig. 3. Performance in a triangle completion task under various cue conditions in young and older participants. (a) Homing accuracy under self-motion cues alone (SM), visual landmarks alone (LM), and with both types of cues available (multiple-cues). Homing accuracy was quantified as the distance between response location and the correct location of a previously visited target. A group-level difference can be observed across all cue conditions. (b) Scatterplot showing mean homing accuracy (target replacement error, RMSE) and performance variability (indexed by the mean standard deviation on the y-axis) in older participants. Colored dashed lines mark the group mean RMSE estimated from the young participants in different cue conditions in panel A. A subgroup of older individuals benefit significantly from the presence of visual landmarks during path integration: in the landmark and double-cue conditions, respectively, more older participants showed reductions in both performance accuracy and variability (mean RMSE and mean standard deviations are positively correlated). Moreover, a relatively higher proportion of older adults reached the performance level closer to the group mean of younger participants under these two conditions as more individual data points from the older age group are clustered around the green [~8] and red lines [~5], in comparison to the self-motion condition. Adapted from Bates and Wolbers (2014).

their performance (e.g., to train older adults to identify and use more reliable navigational cues).

The observation that some older individuals benefit significantly from integrating information from multiple sensory channels corroborates similar findings in nonspatial tasks. For instance, older participants showed greater performance gain in a discrimination task when stimuli were presented in both visual and auditory modalities as compared to when stimuli were presented in the single modality (Laurienti, Burdette, Maldjian, & Wallace, 2006). In addition, such performance gain was significantly more evident in the aged group than in young participants. Hence, although PI with body-based self-motion cues declines with advancing age even for some older superior performers, being able to encode locations relative to external landmarks or more optimal cue integration could help to offset such age-related deficits.

1.1.2. *Landmark and route knowledge*

The two fundamental elements of landmark knowledge include landmark identities (what) and their spatial locations (where, or context information). It has been proposed that what and where information is processed through related but distinct neural circuits within the medial temporal lobe (MTL) (Eichenbaum et al., 2007; Burwell, 2000; but also see Connor & Knierim, 2017). While landmark identity might be encoded in the perirhinal and lateral entorhinal cortices (LECs, Burke et al., 2014), the spatial context pertaining to the information where the landmark is experienced might be encoded primarily in the parahippocampal and medial entorhinal cortices (MECs, Reagh & Yassa, 2014). However, some studies have also reported that the segregation of the two pathways is not absolute (Van Strien, Cappaert, & Witter, 2009). For example, human anterolateral entorhinal cortex (EC) volume (alERC, analogous to rodent LEC) has been associated with object-in-place memory in older adults (Yeung et al., 2019).

Dissociations between identity memory and location/contextual memory for landmarks have been reported in older adults. Reagh et al. (2016) examined recognition memory of objects and 2D spatial-locations in young (18–27 years) and older (60–83 years) participants. The older age group was further divided into aged impaired (AI) and aged unimpaired (AU) subgroups based on their episodic memory performance (note that the AI group still scored within their age-based norm). The AU group showed comparable performance to their younger counterparts in recognition of 2D locations, regardless of the degree of similarity between the test and study locations, but they had more difficulty in the object recognition task. In contrast, this advantage for spatial location/context discrimination was not observed in the AI group.

Interestingly, LEC has been shown to be even more vulnerable in advanced age and during the course of Alzheimer's disease (AD) pathology (Reagh & Yassa, 2017; Khan et al., 2013), in comparison to MEC. In addition, alERC volume has been linked to cognitive decline in aging prior to clinical diagnosis (Olsen et al., 2017). Since episodic memory is composed of "What," "Where," and "When" knowledge, one could speculate that superior episodic memory observed in the AU group might be partially attributed to better location/spatial memory (and possibly, preserved integrity in MEC), despite an age-related deficiency in object memory (and the underlying changes in LEC). However, given that the aforementioned study only tested knowledge of 2D locations on a screen, future studies are needed to examine whether older participants with better episodic memory also have superior location memory for landmarks in a 3D environment. In addition, a direct relation between superior landmark-location memory and superior navigation performance needs to be established.

Route knowledge can be constructed as a sequence of turns associated with landmarks/scenes at corresponding decision points (e.g., a left turn at the intersection of the pharmacy store). The acquisition and recall of such knowledge is a common navigation task in everyday life, thus essential for maintaining autonomy and independence. In general, healthy older adults show a reduced ability to learn and recall routes (Head & Isom, 2010), to retrace a route from end to start (Wiener, Kmecova, & de Condappa, 2012), and to identify correct travel directions when approaching a learned intersection from a novel perspective (Wiener, de Condappa, Harris, & Wolbers, 2013). However, some older adults showed superior performance in various route-knowledge tasks. For instance, some older participants demonstrated exceptional landmark-action associative memory (i.e., knowledge of travel directions associated with the landmarks at intersections) as well as landmark sequence memory after learning routes in a desktop VE (Hilton, Johnson, Slattery, Miellet, & Wiener, 2021).

Moreover, eye-tracking data suggest that older good route-learners, similar to their younger counterparts, employed more exploratory gaze behavior when approaching an intersection; in contrast to a more spatially focused gaze behavior when traveling between the straight segments in between intersections (Hilton, Miellet, Slattery, & Wiener, 2020). These findings suggest that employing appropriate learning strategies (e.g., being attentive to task-relevant information in one's surroundings) might be one way older superior navigators resort to mitigate the negative consequence of aging. It is, thus, worthwhile to look into the learning strategies used by older superior navigators. Such knowledge would be informative in designing intervention programs where older adults with normal and pathological age-related declines could be instructed and trained to employ efficient navigation strategies.

1.1.3. Allocentric spatial learning and cognitive mapping

Egocentric spatial learning and representations are generally spared in older adults, whereas age-related deficits have been reported in allocentric spatial processing (Colombo et al., 2017; Van der Ham, Claessen, Evers, & van der Kuil, 2020). Yet, empirical studies do point toward evidence of well-preserved allocentric spatial memory in some older adults (Merhav & Wolbers, 2019; Zhong et al., 2017). The Morris water maze (MWM) is a classic paradigm to assess allocentric spatial learning and retrieval, where a hidden target location needs to be learned in relation to environmental cues.

Declining performance in the MWM is generally associated with advancing age (Driscoll et al., 2003; Moffat & Resnick, 2002). Using a desktop virtual MWM task, Zhong et al. (2017) looked specifically at the search patterns of good-performing and poor-performing older adults (based on a median split of performance scores from the older age group, Fig. 4a). Older good performers showed performance similar to their younger counterparts across multiple measures, including search accuracy (Fig. 4b) and escape latency (Fig. 4c). In addition, regardless of their MWM performance, participants were comparably able to move around in the virtual environment (Fig. 4d), suggesting that superior performance in the good performers could not simply be attributed to better visuo-motor abilities. These results indicate that successful maintenance of allocentric spatial coding might be one of the key features that distinguishes older superior performers from their peers with normal age-related declines.

In addition to being encoded in different reference frames, spatial information can also be acquired from different types of learning experience. We can learn a city layout through an active exploration, where a variety of perceptual experiences are integrated to form a coherent representation of our surroundings (e.g., visual landmarks combined with PI). Alternatively, we can also acquire spatial information by studying a 2D map of the city. Successful navigation often relies on the flexible coordination of different learning modalities.

Age-related deficits have been commonly observed in switching between different forms of spatial learning and representations (Rodgers, Sindone, & Moffat, 2012; Harris, Wiener, & Wolbers, 2012), but older superior navigators might be able to defeat such an age-related decline. For example, Yamamoto and Degirolamo (2012) assessed knowledge about allocentric spatial relations among landmarks. Both young and older adults learned the spatial layout of multiple landmarks either via virtual exploration from a ground-level perspective in VE (upper panel in Fig. 5a) or from a map of the same VE (lower panel in Fig. 5a).

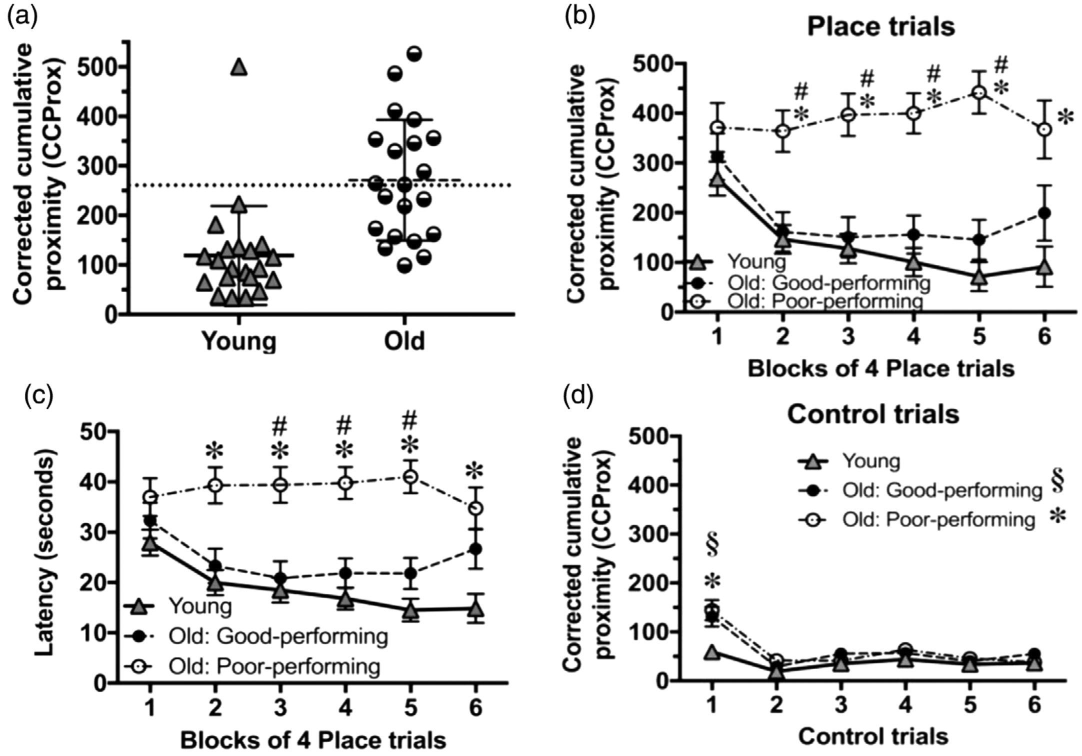

Fig. 4. Virtual MWM performance of young, good-performing, and poor-performing older adults in Zhong et al. (2017). (a) Overall age-related group difference in search errors when locating a hidden target in the virtual MWM. Within the older age group, participants were further split into good performers and poor performers based on the group median indicated by the dashed line. (b) Search errors across trials of the three groups. Both young and good-performing older adults improved their search accuracy with learning, and performance was comparable between the two groups. However, poor-performing older adults did not display such learning-induced improvement. (c) Search latency, the time taken to reach the hidden platform, across trials in the three groups. Similar to the observations from search accuracy, young and good-performing older participants became more efficient in locating the target through learning. Conversely, such learning-related changes were not observed in the poor-performing older participants. (d) Search errors of the three groups across control trials where the target was visible. Group differences diminished, indicating that the three groups of participants, regardless of their age and allocentric place learning performance, were equivalent in their visuomotor ability. Adapted from Zhong et al. (2017).

Although both age groups performed equally well in the map-learning condition, better performance was observed in the younger group as well as in some older individuals under the ground-level navigation condition (Fig. 5b). The observation that the ground-level navigation learning condition not only distinguished the memory performance between the age groups but also between the good and poor navigators within the older age group is particularly informative. These good performers might benefit from superior cognitive mapping during which view-dependent egocentric knowledge was transferred to form view-independent allocentric knowledge.

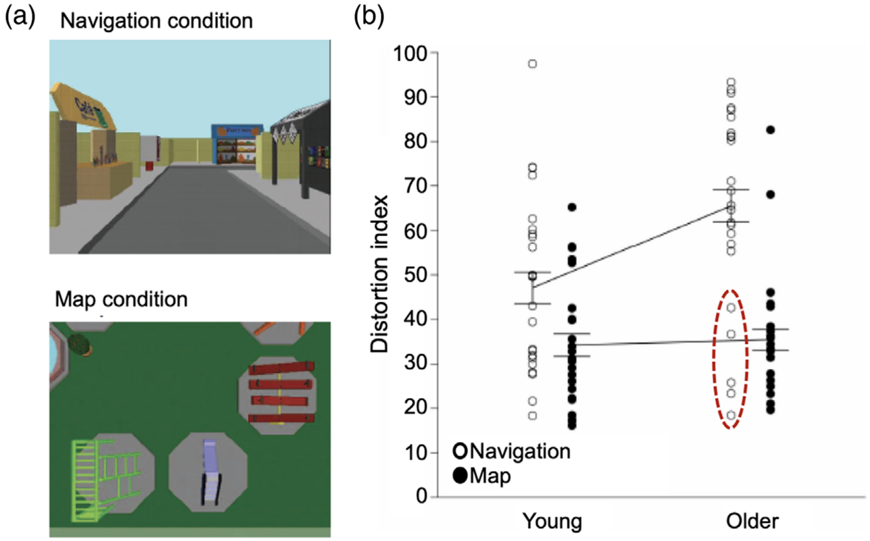

Fig. 5. Virtual environments learned by participants in Yamamoto and DeGirolamo (2012) and memory performance on the spatial layout of the VEs in young and older participants. (a) Participants learned the locations of landmarks in desktop VEs, either from a ground-level perspective in the navigation condition (upper panel) or from an aerial perspective in the map condition (only a subset of landmarks were visible at a time; lower panel). (b) During the memory test, participants were asked to replace the landmarks on a 2D board. The distortion index reflects the fit between participants' reconstructed layout and the correct landmark layout, with smaller values indicating more accurate memory. Although an age-related group difference was observed in the navigation condition, five older participants were even more accurate in reconstructing the landmark layout than the group average of young participants. In contrast, no group difference was observed when the VE was learned from the map. Adapted from Yamamoto and DeGirolamo (2012).

The advantage of cognitive mapping ability in subsets of older adults also provides an important clue to understanding why age-related deficits are pronounced in some route-learning tasks where more egocentric-to-allocentric transformation is involved. For instance, the retracing and redirection tasks mentioned above rely on the successful recognition of routes/scenes from a novel perspective, independent of the egocentric learning experience. Older adults, in general, have more difficulty in these tasks compared to the route repetition task in which no perspective change is required.

The behavioral studies summarized above indicate that some older individuals exhibit exceptional, in some cases even youth-like performance in PI, acquisition of landmark and route knowledge, allocentric spatial learning, and cognitive mapping, which would serve as the foundation for achieving more complex wayfinding tasks.

1.2. *Preserved* domain-independent cognitive abilities *contributing to superior navigation/spatial memory in late adulthood*

Like any complex cognitive task, spatial learning and navigation involve both domain-specific (e.g., coding of distance and direction information) as well as other perceptual and cognitive abilities (e.g., executive processes) generally involved in most cognitive tasks.

Superior navigation performance could hence be a result of excellence in one or multiple processes/domains. Given what is known about the cognitive processes involved in spatial learning/memory and navigation, in this section, we explore possible domain-independent cognitive correlates that may contribute to preserved, sometimes even youth-like, navigation performance in advanced age.

Mental imagery, the ability to reconstruct and manipulate perceptual experiences into imagery, is a key component of human cognition. Imagining the past and future has been linked to spatial memory and navigation in that imagery is hypothesized to have overlapping neural underpinnings with spatial memory and navigation (Bicanski & Burgess, 2018; Chersi, Donnarumma, & Pezzulo, 2013). Using our mental spatial representation for planning navigation involves imagining past and future navigation experience. Mental imagery skills, such as mental rotation, have been shown to correlate with navigation performance (Palermo, Iaria, & Guariglia, 2008), and imagery processes are selectively affected by aging (Dror & Kosslyn, 1994). In the case of older superior navigators, preserved imagery skills might facilitate successful navigation. Results from one cognitive training study support this speculation in that older participants who were instructed to use an imagery strategy during route learning outperformed the control group without instruction, especially in those spatial memory tasks that demanded active manipulation of learned spatial information (Carbone, Meneghetti, & Borella, 2021).

Executive functions (EFs) and attention represent another nonspatial, domain-independent cognitive mechanism necessary for goal-directed navigation. EFs encompass a wide range of abilities, including inhibition, interference control (selective attention and cognitive inhibition), working memory (WM), and cognitive flexibility (Diamond, 2013). With respect to goal-directed navigation, EFs and attention are critically involved when we (1) need to maintain a navigational goal in mind while planning and evaluating different route options, (2) selectively attend to various environmental stimuli that are most relevant to a current navigational goal, and (3) switch between navigation strategies in response to changes in task demands and/or the environment (Zhong & Moffat, 2018).

Similar to spatial memory and navigational abilities, these core EFs also decline during normal aging in that older adults are relatively poor at inhibiting distractions and task switching (Diamond, 2013). Interestingly, it has been shown that test scores on EFs predicted virtual MWM performance of older participants (mean age of 68 years; Moffat, Kennedy, Rodrigue, & Raz, 2007), suggesting a beneficial role of superior EFs in maintaining superior navigation performance in old age. Possibly, older superior navigators with preserved EFs might benefit from enhanced selective attention to task-relevant cues and efficiently adjusting to changing task demands/goals during navigation.

WM, the ability to maintain and manipulate information in mind, is needed in various spatial tasks, including PI (Shrager, Kirwan, & Squire, 2008) and route learning (Lester, Moffat, Wiener, Barnes, & Wolbers, 2017, Blacker, Weisberg, Newcombe, & Courtney, 2017). This ability is also particularly relevant in transferring egocentric spatial knowledge into an allocentric map representation (e.g., manipulating and integrating different views into a coherent representation). WM is predictive of pointing task performance of older participants after route learning (Richmond, Sargent, Flores, & Zacks, 2018). In particular, spatial WM, the ability to maintain location and spatial-relational information, is correlated with route integration performance (Blacker et al., 2017).

Taken together, the studies reviewed here point to an important role of preserved general cognitive abilities in support of exceptional navigation/spatial memory performance in old age. Future studies are needed to fully characterize the cognitive profiles of older superior navigators as well as to examine the relative contributions of various domain-independent cognitive variables to youth-like navigational/spatial memory abilities in late adulthood.

2. Potential neural mechanisms underlying superior navigation/spatial memory performance in late adulthood

The neural circuitry underlying spatial navigation and memory is complex, encompassing a network of key structures in MTL (e.g., the hippocampus and the neighboring parahippocampal cortex, EC), various cortical (e.g., retrosplenial and parietal cortex, prefrontal cortex [PFC]), and subcortical structures (e.g., thalamus and striatum). Part of this network is responsible for navigation-specific spatial processing, such as place coding via place cells in the hippocampus, directional coding via head-direction cells in the thalamus and retrosplenial cortex (RSC), self-motion and position coding via grid cells in the entorhinal and parietal cortex in support of PI, and scene processing in the parahippocampal area (for reviews on the neural underpinnings for navigation and spatial memory, see, e.g., Chersi & Burgess, 2015; Ekstrom, Huffman, & Starrett, 2017).

In the context of aging, MTL structures, such as the EC and hippocampus, are most vulnerable to pathological and normal aging (Lester et al., 2017). However, in the case of older superior navigators, existing evidence from the cognitive aging literature has led to our speculation that the aging navigational network might engage various protective mechanisms to cope with such deleterious consequences (Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012, Cabeza et al., 2018). For example, older superior navigators might not experience age-related degradation in key structures of the spatial network (e.g., the MTL), in contrast to the declines seen in normal aging. Such a possibility would speak to the presence of brain resilience in advanced age. Alternatively, the navigational network might reorganize to promote cognitive enhancement, both in the form of enhanced activity in the key regions and widespread activation in areas beyond these key regions. Therefore, understanding how these protective mechanisms are coordinated in the navigational circuits would provide a unique insight into successful cognitive aging.

Indeed, several longitudinal studies have reported interindividual variability in the development of age-related neurochemical, structural, and functional changes in the brain (Nyberg et al., 2012). For example, some older adults have larger hippocampal volumes (Lupien et al., 2007) compared to younger adults and show less annual hippocampal volume change (Fjell et al., 2009), which is in contrast to volume shrinkage often seen in normal aging. Similar patterns have been reported in other cortical and subcortical structures (Nyberg et al., 2010; Raz et al., 2005). In one longitudinal fMRI study, which followed participants (55–79 years) over a span of 20 years with two fMRI measurements spaced 6 years (Persson, Kalpouzos, Nilsson, Ryberg, & Nyberg, 2011), BOLD signals in the left hippocampus were maintained for those individuals with stable episodic memory performance while showing a decrease in those with declining memory performance.

With respect to the neurotransmitter systems, dopamine loss has been commonly linked to age-related declines in multiple cognitive domains. However, individual differences in dopamine binding persist in old age. For example, Rieckmann et al. (2011) found that some older adults, in contrast to the group-level reduction, showed preserved relationships of D1 binding in sensorimotor and frontal regions, and these individuals also demonstrated "youth-like" performance in an interference resolution task. Although these findings are not explicitly related to navigational/spatial memory abilities, they support the notion that similar interindividual variabilities in neurochemical/structural/functional integrity of the aging navigational network could be present.

2.1. *Preserved* spatial coding *in the aging brain*

Successful retention of superior navigational abilities in some older individuals could be a result of successful preservation of the integrity of the navigational system, related to the notion of brain maintenance (Nyberg et al., 2012). For instance, hippocampal perfusion was negatively correlated with reaction time on the spatial memory task in older adults, suggesting the importance of physiological integrity in the aging hippocampus for maintaining superior spatial memory (Heo et al., 2010).

Furthermore, functional integrity within the navigational network also likely contributes to the preservation of spatial learning and memory in late adulthood. Diersch, Valdes-Herrera, Tempelmann, and Wolbers (2021) investigated learning-related dynamics within the key regions of the aging navigational network. Specifically, young and older participants learned the spatial layout of a virtual town and performed pointing tasks while undergoing fMRI scanning. Although an overall age difference was observed in both behavioral performance and functional activations, the top and good learners in the older age group, similar to the young participants, exhibited learning-related activity reduction in several brain regions, including the anterior hippocampus. In addition, increased activity was observed in the RSC, which corresponded to the progression of the behavioral learning curves. Moreover, older superior learners also demonstrated stronger inhibitory self-connections in the anterior hippocampus compared to older poor learners, mirroring the connectivity patterns observed in the young participants. As aging has been associated with aberrant intrinsic excitability in the hippocampus (Thomé, Gray, Erickson, Lipa, & Barnes, 2016), the results from Diersch et al. (2021) hint at the contribution of preserved excitatory-inhibitory balance in the aging MTL to the maintenance of successful spatial learning and cognitive mapping.

In addition to the hippocampus, EC is another crucial area responsible for spatial coding in that the grid cell system encodes positional information (Hafting, Fyhn, Molden, Moser, & Moser, 2005; Doeller, Barry, & Burgess, 2010; Stangl et al., 2018). The EC is affected by age-related pathology such as tau deposition even earlier than the hippocampus (Braak & Braak, 1991; Stranahan & Mattson, 2010). Combining a behavioral PI task with functional MRI, Stangl et al. (2018) showed that older adults had compromised grid-cell-like representations

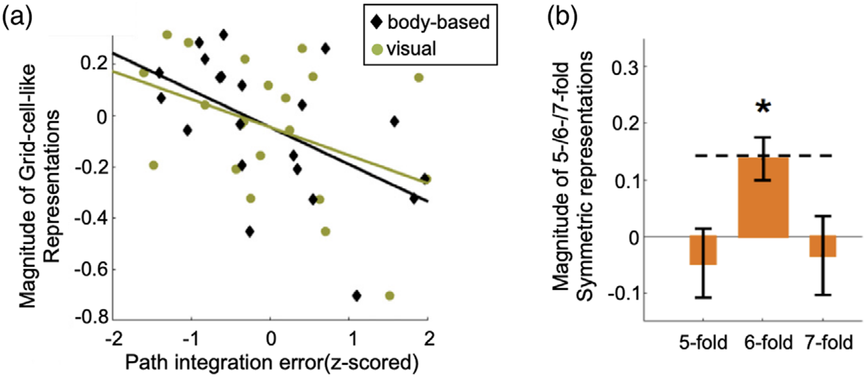

Fig. 6. Superior path integration performance in older participants linked to "youth-like" grid-cell-like representation. (a) Within older participants, path integration error was negatively correlated with the magnitude of grid-cell-like signals measured in fMRI. Importantly, individuals with "youth-like" grid-cell-like representations (in the range of 0–0.2) also exhibited superior performance compared to their peers. (b) The subgroup of older participants who were top-performers in path integration with body-based self-motion cues had preserved grid-cell-like representation in EC, the magnitude of its six-fold symmetry on par with the group average of their younger counterparts. Dashed line indicates the mean grid-cell-like representation magnitude of healthy young controls. Adapted from Stangl et al. (2018).

in the EC, which was linked to poorer PI performance compared to the young participants. Interestingly, within older participants, PI performance was significantly correlated with the magnitude of grid-cell-like representations (Fig. 6a). Moreover, the top-performers in the older age group also showed well-preserved grid-cell-like representations in the EC (Fig. 6b). Together, these results indicate that preserved grid cell functions in the EC are critical for superior PI performance in late adulthood.

Superior navigation performance in late adulthood might also be achieved through compensatory mechanisms that are adaptive to the evolving brain changes, pointing to an age-related reorganization of the functional brain networks. Specifically, increased engagement of extra-hippocampal regions in solving spatial tasks has been observed in the aging brain, including the caudate, PFC, parietal cortex, and RSC (Moffat, Elkins, & Resnick, 2006; Moffat et al., 2007). For instance, older good performers in a virtual MWM task had greater activations in prefrontal regions compared to older poor performers (Reynolds, Zhong, Clendinen, Moffat, & Magnusson, 2019). Moreover, increased connectivity between the parahippocampal place area (PPA) and the occipital cortex and decreased connectivity between the lower-level visual area and the hippocampus have been observed in older adults in comparison to young participants. In response to the functional decline of the hippocampus through aging, such changes in connectivity suggest a putative compensatory role of the PPA in navigation-relevant visual-scene processing (Ramanoël et al., 2019).

Beyond the MTL, PFC, in particular, the medial PFC is critically involved in navigation-relevant computations (Spiers, 2008; Ito, 2018) and shares extensive reciprocal connections with other key regions of the navigational network, such as the hippocampus, EC, and striatum (Euston, Gruber, & McNaughton, 2012). For instance, cells in the medial PFC seem to represent goal locations (Hok, Save, Lenck-Santini, & Poucet, 2005; Negrón-Oyarzo et al., 2018), and a human patient with damage to the ventromedial PFC showed difficulty in wayfinding but was able to successfully navigate if the goal location was repeatedly reminded (Ciaramelli, 2008). Thus, the PFC might be essential in keeping the goal destination in WM and assisting route planning/action monitoring to reach the goal.

With regard to aging, the PFC shows a loss of NMDA receptors and increased inhibition of pyramidal cells due to GABAergic changes (Carpenter, Kelly, Bizon, & Frazier, 2016; McQuail et al., 2016). Furthermore, age-related decrease in the PFC gray matter volume has been observed in nonhuman primates (Alexander et al., 2008) and humans (Storsve et al., 2014). Therefore, successful navigation and spatial memory performance in late adulthood might be related to the preserved function of the PFC as well as its interactions with the hippocampus in response to age-related alterations. Indeed, larger gray and white matter volumes in the PFC were associated with better virtual MWM performance in older participants (Moffat et al., 2007), hinting at the contribution of the structural integrity in the PFC to superior navigation/spatial learning in some older individuals.

Theta rhythm, a ∼4–12 Hz oscillation observed in the local field potential, is another behaviorally and cognitively relevant physiological signature linked to learning and memory, including episodic memory and spatial navigation (see Buzsáki & Moser, 2013, and Herweg, Solomon, & Kahana, 2020 for a discussion of the functional role of the theta rhythm in complex cognitive processes). In the context of human navigation and spatial memory, theta oscillations have been reported in the MTL, including the hippocampus and parahippocampal gyrus (Ekstrom et al., 2005), as well as in cortical networks, such as the PFC and parietal cortex (Kaplan et al., 2014). Theta oscillations across the MTL are responsive to spatial views during goal-directed navigation or spatial updating (Ekstrom et al., 2005; Watrous, Fried, & Ekstrom, 2011). Right hippocampal/parahippocampal theta activity is found to be modulated by the spatial configuration of an environment in a virtual MWM task (Pu, Cornwell, Cheyne, & Johnson, 2017). Moreover, an increase in theta power in the hippocampus and parahippocampal gyrus precedes the retrieval of spatial information after learning a spatial layout (Herweg et al., 2020).

In the context of aging, reduced theta and alpha oscillations in the left frontal cortex are correlated with poorer cognitive mapping performance in older participants (Lithfous et al., 2015). In contrast, older high performers who exhibited superior accuracy in a virtual-maze navigation task had greater theta activity in the parahippocampal gyrus than younger controls (Lithfous, Dufour, Bouix, Pebayle, & Després, 2018). This finding, together with heightened functional connectivity between the PPA and visual areas, suggests a potential compensatory role of the parahippocampal area in response to the aging hippocampus, in that the navigational network might rely more on extra-hippocampal resources.

The evidence reviewed above converges on the idea that the aging brain engages various protective mechanisms in a dynamic way to achieve superior performance in late adulthood. In the case of superior navigators, both maintenance of the navigational network (e.g., preserved structural/functional integrity in the hippocampus and EC) and functional reorganization of the network (e.g., the compensatory roles of the parahippocampal gyrus, including PPA, and the prefrontal area in relation to hippocampal declines) have been shown to contribute to superior spatial navigation/memory performance in some older individuals. Thus, examining how these protective mechanisms jointly support the performance of older superior navigators would be particularly informative for understanding cognitive aging in general.

2.2. Preserved offline ripple activities *contributing to successful consolidation of* allocentric spatial memory

The above discussions highlight the potential significance of both maintenance and compensatory mechanisms during "online" encoding of spatial information. Another possible contributing factor toward superior navigation in old age might be highly preserved memory consolidation. In rodents, temporally coordinated cortical-hippocampal reactivation is observed during sharp-wave ripples (SWRs), short bouts (40–120 ms) of high-frequency (140–250 Hz) oscillations, in postlearning sleep and rest periods. Such reactivation patterns correlate with the cell firing patterns activated along a trajectory during spatial learning (i.e., memory replay; for review, see Ólafsdóttir, Bush, & Barry, 2018; Buzsaki, 2015). Moreover, disruptions of these offline reactivations impair subsequent retrieval of spatial memory (Jadhav, Rothschild, Roumis, & Frank, 2016). Intracranial recordings in humans have also reported similar SWR activities (though in humans, the frequency tends to be lower, $\sim$100 Hz; Bragin, Engel, Wilson, Fried, & Mathern, 1999). Such ripple events are observed during both quiet rest and nonrapid eye movement sleep and tend to co-occur with cortical slow waves (Axmacher, Elger, & Fell, 2008; Logothetis et al., 2012).

In the context of normal aging, sleep physiology, as well as brain structures and neuromodulatory processes supporting consolidation mechanisms during sleep, are altered. For instance, aged rats have fewer and less reliable ripple activities during postlearning rest (Wiegand et al., 2016), suggesting a reduction in both quantity and quality of learning-induced reactivations. Such age-related disruptions of postlearning SWRs might compromise memory consolidation and consequently lead to impaired spatial memory (Muehlroth & Werkle-Bergner, 2020; Harand et al., 2012).

One study examined sleep-related spatial memory benefits in young and older adults (Varga et al., 2016). Participants learned a target location while navigating through a virtual maze, and their memory of the spatial layout of the maze was assessed both before and after polysomnographically recorded sleep. At the group level, older participants performed worse and did not exhibit significant improvements in maze performance after sleep. Corresponding to the lack of overnight performance change, sleep quality in the older age group was characterized by a decreased amount and increased fragmentation of slow-wave sleep. However, regardless of age groups, frontal slow-wave activity (SWA) was positively correlated with overnight performance change (Fig. 7a), as well as medial prefrontal cortical volume across all participants (Fig. 7b). Critically, some older participants (highlighted by the red circle in Fig. 7a) who had the highest proportion of SWA (within their age group) also demonstrated the largest overnight improvement in virtual maze performance.

Slow-wave oscillations are thought to help orchestrate the cortical-hippocampal dialogue by synchronizing SWR-associated reactivations with thalamo-cortical spindles, which drives

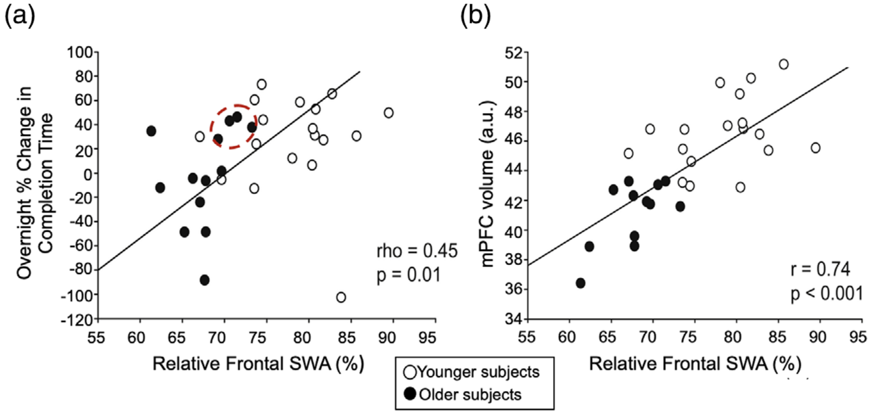

Fig. 7. Relative frontal slow-wave activity (SWA) positively correlates with overnight performance improvement in spatial memory (a) as well as medial PFC volume (b) across all participants. In particular, a subset of older participants exhibited a similar amount of overnight improvement (highlighted in the dotted-line circle) as compared to young participants. Correspondingly, these older adults also had the highest proportion of SWA in their age group. Adapted from Varga et al. (2016).

the transfer of memory traces toward the neocortex for long-term storage (Buzsaki, 1996). The correlation between frontal SWAs and spatial memory performance observed in Varga et al. (2016) suggests: (1) an important role of the frontal areas, including the PFC in memory consolidation and retrieval; and (2) the crucial contribution of preserved slow-wave-associated memory consolidation processes in maintaining superior spatial memory in old age. It will be important to determine, with a combination of sleep recordings, functional neuroimaging, and memory assessment, if the memory consolidation mechanisms, including sharp wave ripple-associated replays and their interactions with the frontal-lead slow-wave oscillations, remain intact in older superior navigators with "youth-like" spatial memory.

2.3. Preserved synaptic plasticity contributing to allocentric spatial learning

Closely related to the electrophysiological processes (co-occurrence of experience reactivations in the hippocampus and neocortex) taking place in memory consolidation, synaptic plasticity also plays a key role in information storage, including spatial memory formation. Aging has a broad impact on synaptic communication and plasticity regulation, including transmitter systems and intracellular signaling pathways, which in turn results in deficits in learning and memory. Here, we briefly review evidence from the rodent literature as well as recent in-vivo imaging studies with older adults, highlighting the importance of preserved synaptic plasticity in successful cognitive aging (the mechanism through which synaptic plasticity induces long-term/short-term memory is beyond the scope of this paper, but for reviews, see Neves, Cooke, & Bliss, 2008; Takeuchi, Duszkiewicz, & Morris, 2014; also see Lester et al., 2017 for a discussion in the context of aging).

Intact coordination of presynaptic and postsynaptic glutamatergic components in the hippocampus and its adjacent cortex has been linked to the successful formation of spatial memories in late adulthood. For example, aged rats with intact allocentric spatial memory in the MWM show maintained postsynaptic ionotropic glutamate receptor levels in the hippocampal-adjacent cortex, similar to those of young rats (Ménard et al., 2015). Furthermore, aged rats of the obesity-resistant LOU strain (this strain is marked by intact memory despite aging) also had glutamatergic receptors and presynaptic vesicular glutamate transporter levels on par with those of young rats.

Furthermore, sustained long-term depression, a form of synaptic plasticity critical for learning and memory, is also observed in the associative/commissural inputs to CA3 of aged rats with intact MWM performance (Yang et al., 2013). In addition, youth-like synaptic protein expression is preserved in the hippocampal complex of aged-unimpaired rats, such as preserved PRDX6 levels in the dentate gyrus and elevated hippocampal BDNF (brain-derived neurotrophic factor) mRNA expressions. Such preservation is shown to support intact spatial learning (Lubec et al., 2019; Schaaf et al., 2001). Given that the cognitive mapping ability is critically involved in solving the MWM task, the rodent studies reviewed here provide an important clue to understanding the contribution of preserved synaptic integrity to allocentric memory processing.

Recent advances in in-vivo positron emission tomography (PET) imaging have also brought us corroborating evidence of the importance of synaptic integrity in human cognitive aging. For instance, significant reductions of synaptic density have been reported in the hippocampus of β-amyloid-positive AD patients (Chen et al., 2018), in the right anterior hippocampus extending to the EC in amyloid-positive patients with mild cognitive impairment or AD (Bastin et al., 2020), compared to age-matched healthy controls. Moreover, deficits in hippocampal synaptic vesicle glycoprotein 2A binding (a biomarker for synaptic density) were associated with declines in episodic memory scores (Chen et al., 2018), general cognitive functions, and, interestingly, patients' unawareness of their memory problems (Bastin et al., 2020). Furthermore, a direct link between an increased deposition of tau and a loss of synaptic density has been observed in the MTL of prodromal AD patients (Vanhaute et al., 2019; Becker, Dammicco, Bahri, & Salmon, 2020). Together with the evidence from rodent research, these results reveal a potentially critical role of preserved synaptic plasticity in successful cognitive aging. With the development of new PET tracers, future imaging studies will provide an exciting insight into understanding the molecular mechanisms of synaptic integrity that underlie preserved spatial navigation/memory functioning.

3. How are older superior navigators related to SuperAgers?

As stated in the Introduction, spatial memory/navigation and episodic memory are two highly connected cognitive processes. On the cognitive level, episodic memory consists of information about the location ("Where"), the content ("What"), the temporal context ("When") of one's experience, and the associations among these components (Tulving, 2002). Successful retrieval of episodic memory is thus contingent on successful retrieval of relevant spatial memory, even though not all episodic memories contain spatial components. Mirroring this self-referenced aspect of episodic memory, navigation also contains a strong egocentric coding scheme in which movement and spatial information is often acquired and integrated egocentrically (Buzsáki & Moser, 2013). A recent study provides corroborating behavioral evidence for the link between these two processes because young adults, who performed better in a PI task, also showed better episodic but not better semantic memory (Committeri et al., 2020).

On the level of neural computations, the same neural circuits support both episodic memory and spatial memory/navigation processes, including the MTL, and neocortical areas, such as the parietal cortex and PFC (Hirshhorn, Grady, Rosenbaum, Winocur, & Moscovitch, 2012; Robin et al., 2015; Eichenbaum, 2017). Furthermore, the various types of spatially modulated cells in the hippocampal-entorhinal network are also proposed to play important roles in human episodic memory. In particular, the entorhinal-hippocampal loop might essentially code the topology of experience organized in temporal orders (Rueckemann et al., 2021; Buzsáki & Moser, 2013; Bellmund, Polti, & Doeller, 2020). Furthermore, hippocampal remapping, the phenomenon where hippocampal place cells change their firing fields (or firing rates) in response to environmental changes, has been proposed as a potential mechanism to resolve memory interference both in spatial memory and episodic memory retrieval (Moser, Rowland, & Moser, 2015). Several functional MRI studies with human participants have provided tentative evidence that hippocampal remapping might contribute to the successful retrieval of interfering spatial memory (Kyle, Stokes, Lieberman, Hassan, & Ekstrom, 2015), as well as the successful retrieval of interfering episodic associations between similar scene and object images (Wanjia, Favila, Kim, Molitor, & Kuhl, 2021).

Similar to the development of navigation/spatial memory abilities in late adulthood, episodic memory also deteriorates within the course of normal aging (Shing et al., 2010). For instance, older adults show reduced precision of episodic memory retrieval (Korkki, Richter, Jeyarathnarajah, & Simons, 2020), a deficit in associative binding of episodic features (Shing, Werkle-Bergner, Li, & Lindenberger, 2008), as well as a decline in the cognitive control processes necessary for encoding and retrieval of episodic memory (Shing et al., 2008). These behavioral deficits also correspond to the age-related declines in relevant brain regions (Tromp, Dufour, Lithfous, Pebayle, & Després, 2015; Shing et al., 2008), in particular, the MTL (responsible for associative binding and the vividness of episodic memory recollection) and PFC (responsible for the cognitive control processes), respectively.

However, increased interindividual performance variability in advanced age has also been documented in episodic memory tasks (Nyberg & Pudas, 2019). A subgroup of older adults referred to as SuperAgers with exceptional episodic memory has drawn particular research interest. SuperAgers are typically defined as older adults aged 80+ who show episodic memory on par with or above the average performance of individuals in their 50s and 60s (Rogalski et al., 2013) or even young adults (Hoenig, Willscheid, Bischof, van Eimeren, & Drzezga, 2020).

Given the extensive overlap in the underlying neural resources, it is reasonable to speculate that episodic memory and spatial navigation performance might be highly interconnected. One way to further explore this link is to examine navigational and spatial memory abilities in

SuperAgers as well as episodic memory in older superior navigators. Fully characterizing the cognitive abilities of these two groups of older adults can help to answer whether successful navigation in advanced age could contribute to superior episodic memory (or vice versa).

So far, research has focused on which factors lead to better episodic memory performance in SuperAgers in terms of brain, lifestyle, and genetic differences. To our knowledge, there is no study directly assessing spatial memory and navigation functions in this cohort. However, SuperAgers exhibit a higher degree of structural and functional integrity in various brain regions that are the key sites of the spatial memory/navigational network, including the MTL. For example, when compared to cognitively normal peers, SuperAgers have larger hippocampal volume (Harrison, Maass, Baker, & Jagust, 2018) and larger gray matter volume in the hippocampus, EC, and parahippocampal gyrus. Additionally, they experience reduced gray matter volume loss over time in the same regions (Pascual et al., 2020). Superagers also have many viable neurons in the hippocampal-entorhinal circuits, which may indicate better maintenance of the MTL in relation to successful cognitive aging (Rogalski et al., 2019). Furthermore, they have fewer neurofibrillary tangles in the EC by three-fold, compared to age-matched cognitively normal older adults, and by 100-fold, compared to AD patients. These observations hint at a better maintenance of the EC in this cohort (Gefen et al., 2021).

Similarly, preserved functional integrity of the EC is also observed in superior older navigators. As mentioned in the preceding section, a subgroup of older adults (63–81 years) who performed equally well as their younger counterparts in PI also had preserved grid-cell-like signals in the EC. In contrast, the poor performers in the older age group exhibited reduced magnitude in grid-cell-like representations (Stangl et al., 2018). These results, together with the preserved structural integrity observed in the EC of SuperAgers, lead to the speculation that SuperAgers might also excel in spatial memory/navigation tasks, similar to older superior navigators.

Beyond its role in coding for "spatial-maps," grid-like coding observed in the EC and ventromedial PFC has also been shown to track nonspatial, abstract relations when human participants navigated through conceptual space (Constantinescu, O'Reilly, & Behrens, 2016; Garvert, Dolan, & Behrens, 2017). Considering these studies, the grid cell system, together with hippocampal place cells, might have a broader role in organizing general knowledge and nonspatial experience into relational configurations. Hence, with highly maintained structural and functional integrity of the hippocampal-entorhinal circuit in both SuperAgers and older superior navigators, episodic memory and navigation/spatial memory abilities of the two cohorts might be closely related. The aforementioned study by Reagh et al. (2016) provides preliminary evidence that SuperAgers might indeed be superior navigators. Specifically, older adults with better episodic memory performed comparably to young adults in a 2D spatial discrimination task, demonstrating a potential connection between superior episodic memory and superior spatial navigation abilities in late adulthood.

In addition to the preserved structural and functional integrity of the MTL, SuperAgers also have greater cortical thickness in other core regions of the navigational network, including the anterior cingulate cortex and PFC (Harrison et al., 2012). As previously stated, the PFC is involved in encoding goal locations (Hok et al., 2005; Ito, 2018) and might serve as a compensatory mechanism for spatial navigation in response to age-related negative impacts

(Reynolds et al., 2019). Moreover, both the prefrontal and anterior cingulate cortices are involved in backtracking and reevaluating actions when reorienting during navigation (Javadi et al., 2019). Superior structural and functional integrity in these regions overall might help SuperAgers to succeed in navigation/spatial memory tasks.

Older superior navigators and SuperAgers might be two overlapping groups in that resilience in shared neural resources could ensure preserved performance in both episodic memory and navigation/spatial memory domains. However, given the complexity and multifaceted nature of navigational tasks, superior episodic memory alone is insufficient for achieving exceptional navigation performance. It remains to be seen if older superior navigators and SuperAgers perform similarly in both navigation and episodic memory tasks. Exploring the link between SuperAgers and older superior navigators is particularly important for assessing the connection between episodic memory and spatial navigation, which might shed additional light on hippocampal/MTL functioning in general.

Alternatively, the two groups might not be overlapping in that older superior navigators might show average performance on episodic memory and vice versa. Such results would speak to the importance of rethinking the concept of SuperAgers. Apart from superior episodic memory, superaging might also encompass preservation in other aspects of cognitive functions, including spatial memory/navigation. Future studies can help differentiate the neural, behavioral, and environmental factors leading to these various types of superaging, which would provide a more comprehensive understanding of successful cognitive aging.

4. Future directions

Numerous studies have reported a decline of navigational functioning in healthy aging. However, these comparisons typically look at age effects at the group level, often neglecting the fact that the aging population is tremendously heterogeneous. Converging evidence from studies using a variety of navigation/spatial memory tasks has demonstrated that subgroups of older adults exhibit remarkable navigational abilities on par with their younger counterparts. Such well-maintained abilities might result either from neural computations unaffected by aging or from compensatory mechanisms. We list below some pertinent questions for future studies.

What are the cognitive profiles of superior navigators in advanced age? How do they perform across various spatial learning/navigation tasks? As discussed above, navigation/spatial memory is multifaceted, and different navigation/spatial learning tasks recruit related but differential cognitive processes. Older superior navigators might show individual variability in the types of spatial abilities that are preserved. Characterizing the behavioral/cognitive profiles in this cohort across different types of tasks, both navigation-specific and domain-general (e.g., attention and EFs, mental imagery), would provide further insight into common as well as navigation-specific cognitive resources underlying different spatial learning/navigational processes.

What is the link between superior navigators in late adulthood and SuperAgers? Future studies are needed to compare the behavioral, cognitive, and neurophysiological profiles between the two cohorts to better understand how computations across the MTL contribute to episodic memory and spatial navigation/memory. Furthermore, to draw meaningful comparisons between episodic memory and spatial memory/navigation functioning, it is also necessary to establish spatial memory/navigation tasks with high validity and reliability for large-scale assessments with different age and/or demographical cohorts (corresponding to the standardized assessments already implemented in other cognitive domains).

Even more importantly, longitudinal studies are needed to investigate long-term developmental trajectories of older superior navigators. In the case of normal and pathological aging, cognitive abilities decrease as age progresses, with pathological aging typically leading to a more pronounced decline compared to normal aging. In contrast, successful aging—marked by the absence of impairment in cognition—might be attributed to a larger reserve in spite of a comparable decline compared to the progression observed in normal agers, to differential developmental trajectories, or to a combination of both possibilities (Fig. 1a). For instance, do older superior navigators already perform exceptionally well compared to their peers in early and middle adulthood despite experiencing an amount of decline similar to normal agers? Or do these individuals experience a slower-than-average decline, albeit equivalent performance in early adulthood in comparison to normal performers? These possibilities speak to different protective mechanisms that the brain engages in response to the deleterious consequences of aging. Tracing the long-term progression of spatial navigation abilities in older superior navigators as well as normal agers is thus essential for understanding the development of their spatial cognition across the lifespan.

Both animal and human research have provided tremendous insight into age-related changes in the cellular-, molecular-, and network-level mechanisms underlying spatial cognition and episodic memory and the subsequent behavioral outcomes (i.e., changes in task performances). However, the behavioral paradigms used to assess navigation/memory functions across the two disciplines are often not fully consistent regarding the cognitive processes they tap into. For example, whether the navigation tasks used in rodent studies reflect the same complexity of the cognitive processes involved in navigation tasks used in human studies, or, what an equivalent episodic memory task would be in the context of animal research, would have a direct impact on how well the cellular/molecular findings (usually based on animal studies) could translate to the network-level results (usually based on human fMRI studies). Such inconsistency in the behavioral paradigms can make it difficult to obtain conclusive evidence for understanding the fundamental mechanisms underlying cognitive aging. Moving forward, it would be particularly worthwhile for the field to establish comparable navigation/memory tasks that are suitable for both human and animal studies in order to bring a synergized understanding of cognitive aging from across the neurochemical, cellular, and network systems.

Finally, understanding how navigational abilities are well maintained in older superior performers would be especially helpful for promoting successful aging in the broader population. Spatial navigation is ubiquitous in daily life, and being able to find our way is essential for maintaining a sense of autonomy and independence. Older adults often report a decrease in their navigational abilities, which can lead to compromised mobility and decreased psychological well-being. Unveiling the “secrets” that work for older superior navigators, including efficient navigation strategies and relevant lifestyle factors, is the first step toward designing evidence-based, targeted intervention/cognitive training programs for "normal agers."

References

Adamo, D. E., Briceño, E. M., Sindone, J. A., Alexander, N. B., & Moffat, S. D. (2012). Age differences in virtual environment and real world path integration. *Frontiers in Aging Neuroscience*, *4*(26), 1–9. https://doi.org/10.3389/fnagi.2012.00026

Alexander, G. E., Chen, K., Aschenbrenner, M., Merkley, T. L., Santerre-Lemmon, L. E., Shamy, J. L., … Barnes, C. A. (2008). Age-related regional network of magnetic resonance imaging gray matter in the rhesus macaque. *Journal of Neuroscience*, *28*(11), 2710–2718. https://doi.org/10.1523/JNEUROSCI.1852-07.2008

Allen, G. L., Kirasic, K. C., Rashotte, M. A., & Haun, D. B. M. (2004). Aging and path integration skill: Kinesthetic and vestibular contributions to wayfinding. *Perception and Psychophysics*, *66*(1), 170–179. https://doi.org/10.3758/BF03194870

Axmacher, N., Elger, C. E., & Fell, J. (2008). Ripples in the medial temporal lobe are relevant for human memory consolidation. *Brain*, *131*(7), 1806–1817. https://doi.org/10.1093/brain/awn103

Bastin, C., Bahri, M. A., Meyer, F., Manard, M., Delhaye, E., Plenevaux, A., … Salmon, E. (2020). In vivo imaging of synaptic loss in Alzheimer's disease with [18F]UCB-H positron emission tomography. *European Journal of Nuclear Medicine and Molecular Imaging*, *47*(2), 390–402. https://doi.org/10.1007/S00259-019-04461-X

Bates, S. L., & Wolbers, T. (2014). How cognitive aging affects multisensory integration of navigational cues. *Neurobiology of Aging*, *35*(12), 2761–2769. https://doi.org/10.1016/j.neurobiolaging.2014.04.003

Becker, G., Dammicco, S., Bahri, M. A., & Salmon, E. (2020). The rise of synaptic density PET imaging. *Molecules*, *25*(10), 2303. https://doi.org/10.3390/MOLECULES25102303

Bellmund, J. L. S., Polti, I., & Doeller, C. F. (2020). Sequence memory in the hippocampal–entorhinal region. *Journal of Cognitive Neuroscience*, *32*(11), 2056–2070. https://doi.org/10.1162/jocn_a_01592

Bicanski, A., & Burgess, N. (2018). A neural-level model of spatial memory and imagery. *eLife*, *7*, e33752. https://doi.org/10.7554/eLife.33752

Blacker, K. J., Weisberg, S. M., Newcombe, N. S., & Courtney, S. M. (2017). Keeping track of where we are: Spatial working memory in navigation. *Visual Cognition*, *25*(7–8), 691–702. https://doi.org/10.1080/13506285.2017.1322652

Braak, H., & Braak, E. (1991). Neuropathological stageing of Alzheimer-related changes. *Acta Neuropathologica*, *82*(4), 239–259. https://doi.org/10.1007/BF00308809

Bragin, A., Engel, J., Wilson, C. L., Fried, I., & Mathern, G. W. (1999). Hippocampal and entorhinal cortex high-frequency oscillations (100–500 Hz) in human epileptic brain and in kainic acid-treated rats with chronic seizures. *Epilepsia*, *40*(2), 127–137. https://doi.org/10.1111/j.1528-1157.1999.tb02065.x

Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). The human hippocampus and spatial and episodic memory. *Neuron*, *35*(4), 625–641. https://doi.org/10.1016/S0896-6273(02)00830-9

Burke, S. N., Maurer, A. P., Nematollahi, S., Uprety, A., Wallace, J. L., & Barnes, C. A. (2014). Advanced age dissociates dual functions of the perirhinal cortex. *Journal of Neuroscience*, *34*(2), 467–480. https://doi.org/10.1523/JNEUROSCI.2875-13.2014

Burwell, R. D. (2000). The parahippocampal region: Corticocortical connectivity. *Annals of the New York Academy of Sciences*, *911*, 25–42. https://doi.org/10.1111/j.1749-6632.2000.tb06717.x

Buzsáki, G. (1996). The hippocampo-neocortical dialogue. *Cerebral Cortex*, *6*(2), 81–92. https://doi.org/10.1093/cercor/6.2.81

Buzsáki, G. (2015). Hippocampal sharp wave-ripple: A cognitive biomarker for episodic memory and planning. *Hippocampus*, *25*(10), 1073–1188. https://doi.org/10.1002/hipo.22488

Buzsáki, G., & Moser, E. I. (2013). Memory, navigation and theta rhythm in the hippocampal-entorhinal system. *Nature Neuroscience*, *16*(2), 130–138. https://doi.org/10.1038/nn.3304

Cabeza, R., Albert, M., Belleville, S., Craik, F. I. M., Duarte, A., Grady, C. L., … Rajah, M. N. (2018). Maintenance, reserve and compensation: The cognitive neuroscience of healthy ageing. *Nature Reviews Neuroscience*, *19*(11), 701–710. https://doi.org/10.1038/s41583-018-0068-2

Campbell, M. G., & Giocomo, L. M. (2018). Self-motion processing in visual and entorhinal cortices: Inputs, integration, and implications for position coding. *Journal of Neurophysiology*, *120*(4), 2091–2106. https://doi.org/10.1152/jn.00686.2017

Carbone, E., Meneghetti, C., & Borella, E. (2021). Supporting route learning in older adults: The role of imagery strategy. *Aging and Mental Health*, *25*(8), 1564–1571. https://doi.org/10.1080/13607863.2020.1727844

Carpenter, H. E., Kelly, K. B., Bizon, J. L., & Frazier, C. J. (2016). Age-related changes in tonic activation of presynaptic versus extrasynaptic γ-amniobutyric acid type B receptors in rat medial prefrontal cortex. *Neurobiology of Aging*, *45*, 88–97. https://doi.org/10.1016/j.neurobiolaging.2016.05.015

Chen, M. K., Mecca, A. P., Naganawa, M., Finnema, S. J., Toyonaga, T., Lin, S. F., … Van Dyck, C. H. (2018). Assessing synaptic density in Alzheimer disease with synaptic vesicle glycoprotein 2A positron emission tomographic imaging. *JAMA Neurology*, *75*(10), 1215–1224. https://doi.org/10.1001/JAMANEUROL.2018.1836

Chersi, F., & Burgess, N. (2015). The cognitive architecture of spatial navigation: Hippocampal and striatal contributions. *Neuron*, *88*(1), 64–77.

Chersi, F., Donnarumma, F., & Pezzulo, G. (2013). Mental imagery in the navigation domain: A computational model of sensory-motor simulation mechanisms. *Adaptive Behavior*, *21*(4), 251–262. https://doi.org/10.1177/1059712313488789

Ciaramelli, E. (2008). The role of ventromedial prefrontal cortex in navigation: A case of impaired wayfinding and rehabilitation. *Neuropsychologia*, *46*(7), 2099–2105. https://doi.org/10.1016/j.neuropsychologia.2007.11.029

Colombo, D., Serino, S., Tuena, C., Pedroli, E., Dakanalis, A., Cipresso, P., & Riva, G. (2017). Egocentric and allocentric spatial reference frames in aging: A systematic review. *Neuroscience & Biobehavioral Reviews*, *80*, 605–621.

Committeri, G., Fragueiro, A., Campanile, M. M., Lagatta, M., Burles, F., Iaria, G., … Tosoni, A. (2020). Egocentric navigation abilities predict episodic memory performance. *Frontiers in Human Neuroscience*, *14*, 574224. https://doi.org/10.3389/FNHUM.2020.574224

Connor, C. E., & Knierim, J. J. (2017). Integration of objects and space in perception and memory. *Nature Neuroscience*, *20*(11), 1493–1503. https://doi.org/10.1038/nn.4657

Constantinescu, A. O., O'Reilly, J. X., & Behrens, T. E. J. (2016). Organizing conceptual knowledge in humans with a gridlike code. *Science*, *352*(6292), 1464–1468. https://doi.org/10.1126/science.aaf0941

Daugherty, A. M., & Raz, N. (2017). A virtual water maze revisited: Two-year changes in navigation performance and their neural correlates in healthy adults. *Neuroimage*, *146*, 492–506. https://doi.org/10.1016/J.NEUROIMAGE.2016.09.044

Diamond, A. (2013). Executive functions. *Annual Review of Psychology*, *64*, 135–168. https://doi.org/10.1146/annurev-psych-113011-143750

Diersch, N., Valdes-Herrera, J. P., Tempelmann, C., & Wolbers, T. (2021). Increased hippocampal excitability and altered learning dynamics mediate cognitive mapping deficits in human aging. *Journal of Neuroscience*, *41*(14), 3204–3221. https://doi.org/10.1523/JNEUROSCI.0528-20.2021

Doeller, C. F., Barry, C., & Burgess, N. (2010). Evidence for grid cells in a human memory network. *Nature*, *463*(7281), 657–661. https://doi.org/10.1038/nature08704

Driscoll, I., Hamilton, D. A., Petropoulos, H., Yeo, R. A., Brooks, W. M., Baumgartner, R. N., & Sutherland, R. J. (2003). The aging hippocampus: Cognitive, biochemical and structural findings. *Cerebral Cortex*, *13*(12), 1344–1351. https://doi.org/10.1093/cercor/bhg081

Dror, I. E., & Kosslyn, S. M. (1994). Mental imagery and aging. *Psychology and Aging*, *9*(1), 90–102. https://doi.org/10.1037/0882-7974.9.1.90

Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*, *30*, 123–152. https://doi.org/10.1146/annurev.neuro.30.051606.094328

Eichenbaum, H. (2017). Prefrontal–hippocampal interactions in episodic memory. *Nature Reviews Neuroscience*, *18*(9), 547–558. https://doi.org/10.1038/nrn.2017.74

Ekstrom, A. D., Caplan, J. B., Ho, E., Shattuck, K., Fried, I., & Kahana, M. J. (2005). Human hippocampal theta activity during virtual navigation. *Hippocampus*, *15*(7), 881–889. https://doi.org/10.1002/hipo.20109

Ekstrom, A. D., Huffman, D. J., & Starrett, M. (2017). Interacting networks of brain regions underlie human spatial navigation: A review and novel synthesis of the literature. *Journal of Neurophysiology*, *118*(6), 3328–3344.

Euston, D. R., Gruber, A. J., & McNaughton, B. L. (2012). The role of medial prefrontal cortex in memory and decision making. *Neuron*, *76*(6), 1057–1070. https://doi.org/10.1016/j.neuron.2012.12.002

Fjell, A. M., Walhovd, K. B., Fennema-Notestine, C., McEvoy, L. K., Hagler, D. J., Holland, D., … Dale, A. M. (2009). One-year brain atrophy evident in healthy aging. *Journal of Neuroscience*, *29*(48), 15223–15231. https://doi.org/10.1523/JNEUROSCI.3252-09.2009

Freiherr, J., Lundström, J. N., Habel, U., & Reetz, K. (2013). Multisensory integration mechanisms during aging. *Frontiers in Human Neuroscience*, *7*, 1–6. https://doi.org/10.3389/FNHUM.2013.00863

Garvert, M. M., Dolan, R. J., & Behrens, T. E. J. (2017). A map of abstract relational knowledge in the human hippocampal–entorhinal cortex. *eLife*, *6*, e17086. https://doi.org/10.7554/eLife.17086

Gefen, T., Kawles, A., Makowski-Woidan, B., Engelmeyer, J., Ayala, I., Abbassian, P., … Geula, C. (2021). Paucity of entorhinal cortex pathology of the Alzheimer's type in SuperAgers with superior memory performance. *Cerebral Cortex*, *31*(7), 3177–3183. https://doi.org/10.1093/cercor/bhaa409

Harand, C., Bertran, F., Doidy, F., Guénolé, F., Desgranges, B., Eustache, F., & Rauchs, G. (2012). How aging affects sleep-dependent memory consolidation? *Frontiers in Neurology*, *3*, 8. https://doi.org/10.3389/fneur.2012.00008

Harris, M. A., Wiener, J. M., & Wolbers, T. (2012). Aging specifically impairs switching to an allocentric navigational strategy. *Frontiers in Aging Neuroscience*, *4*(29), 1–9. https://doi.org/10.3389/fnagi.2012.00029

Harris, M. A., & Wolbers, T. (2012). Ageing effects on path integration and landmark navigation. *Hippocampus*, *22*(8), 1770–1780. https://doi.org/10.1002/hipo.22011

Harrison, T. M., Weintraub, S., Mesulam, M. M., & Rogalski, E. (2012). Superior memory and higher cortical volumes in unusually successful cognitive aging. *Journal of the International Neuropsychological Society*, *18*(6), 1081–1085. https://doi.org/10.1017/S1355617712000847

Harrison, T. M., Maass, A., Baker, S. L., & Jagust, W. J. (2018). Brain morphology, cognition, and β-amyloid in older adults with superior memory performance. *Neurobiology of Aging*, *67*, 162–170. https://doi.org/10.1016/j.neurobiolaging.2018.03.024

Head, D., & Isom, M. (2010). Age effects on wayfinding and route learning skills. *Behavioural Brain Research*, *209*(1), 49–58. https://doi.org/10.1016/j.bbr.2010.01.012

Heo, S., Prakash, R. S., Voss, M. W., Erickson, K. I., Ouyang, C., Sutton, B. P., & Kramer, A. F. (2010). Resting hippocampal blood flow, spatial memory and aging. *Brain Research*, *1315*, 119–127. https://doi.org/10.1016/j.brainres.2009.12.020

Herweg, N., Sharan, A., Sperling, M., Brandt, A., Schulze-Bonhage, A., & Kahana, M. (2020). Reactivated spatial context guides episodic recall. *Journal of Neuroscience*, *40*(10), 2119–2128.

Herweg, N. A., Solomon, E. A., & Kahana, M. J. (2020). Theta oscillations in human memory. *Trends in Cognitive Sciences*, *24*(3), 208–227. https://doi.org/10.1016/j.tics.2019.12.006

Hilton, C., Johnson, A., Slattery, T. J., Miellet, S., & Wiener, J. M. (2021). The impact of cognitive aging on route learning rate and the acquisition of landmark knowledge. *Cognition*, *207*, 104524. https://doi.org/10.1016/j.cognition.2020.104524

Hilton, C., Miellet, S., Slattery, T. J., & Wiener, J. (2020). Are age-related deficits in route learning related to control of visual attention? *Psychological Research*, *84*(6), 1473–1484. https://doi.org/10.1007/s00426-019-01159-5

Hirshhorn, M., Grady, C., Rosenbaum, R. S., Winocur, G., & Moscovitch, M. (2012). Brain regions involved in the retrieval of spatial and episodic details associated with a familiar environment: An fMRI study. *Neuropsychologia*, *50*(13), 3094–3106. https://doi.org/10.1016/j.neuropsychologia.2012.08.008

Hafting, T., Fyhn, M., Molden, S., Moser, M. B., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature*, *436*(7052), 801–806. https://doi.org/10.1038/nature03721

Hoenig, M. C., Willscheid, N., Bischof, G. N., van Eimeren, T., & Drzezga, A. (2020). Assessment of tau tangles and amyloid-β plaques among super agers using PET imaging. *JAMA Network Open*, *3*(12), e2028337. https://doi.org/10.1001/jamanetworkopen.2020.28337

Hok, V., Save, E., Lenck-Santini, P. P., & Poucet, B. (2005). Coding for spatial goals in the prelimbic/infralimbic area of the rat frontal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(12), 4602–4607. https://doi.org/10.1073/pnas.0407332102

Ito, H. T. (2018). Prefrontal–hippocampal interactions for spatial navigation. *Neuroscience Research*, *129*, 2–7. https://doi.org/10.1016/j.neures.2017.04.016

Jadhav, S. P. P., Rothschild, G., Roumis, D. K. K., & Frank, L. M. M. (2016). Coordinated excitation and inhibition of prefrontal ensembles during awake hippocampal sharp-wave ripple events. *Neuron*, *90*(1), 113–127. https://doi.org/10.1016/j.neuron.2016.02.010

Javadi, A. H., Patai, E. Z., Marin-Garcia, E., Margois, A., Tan, H. R. M., Kumaran, D., … Spiers, H. J. (2019). Backtracking during navigation is correlated with enhanced anterior cingulate activity and suppression of alpha oscillations and the “default-mode” network. *Proceedings of the Royal Society B: Biological Sciences*, *286*, 20191016. https://doi.org/10.1098/rspb.2019.1016

Kaplan, R., Bush, D., Bonnefond, M., Bandettini, P. A., Barnes, G. R., Doeller, C. F., & Burgess, N. (2014). Medial prefrontal theta phase coupling during spatial memory retrieval. *Hippocampus*, *24*(6), 656–665. https://doi.org/10.1002/hipo.22255

Khan, U. A., Liu, L., Provenzano, F. A., Berman, D. E., Profaci, C. P., Sloan, R., … Small, S. A. (2013). Molecular drivers and cortical spread of lateral entorhinal cortex dysfunction in preclinical Alzheimer’s disease. *Nature Neuroscience*, *17*(2), 304–311. https://doi.org/10.1038/nn.3606

Knierim, J. J., & Hamilton, D. A. (2011). Framing spatial cognition: Neural representations of proximal and distal frames of reference and their roles in navigation. *Physiological Reviews*, *91*(4), 1245–1279. https://doi.org/10.1152/physrev.00021.2010

Korkki, S. M., Richter, F. R., Jeyarathnarajah, P., & Simons, J. S. (2020). Healthy ageing reduces the precision of episodic memory retrieval. *Psychology and Aging*, *35*(1), 124–142. https://doi.org/10.1037/PAG0000432

Kyle, C. T., Stokes, J. D., Lieberman, J. S., Hassan, A. S., & Ekstrom, A. D. (2015). Successful retrieval of competing spatial environments in humans involves hippocampal pattern separation mechanisms. *eLife*, *4*, e10499. https://doi.org/10.7554/eLife.10499

Laurienti, P. J., Burdette, J. H., Maldjian, J. A., & Wallace, M. T. (2006). Enhanced multisensory integration in older adults. *Neurobiology of Aging*, *27*(8), 1155–1163. https://doi.org/10.1016/j.neurobiolaging.2005.05.024

Lester, A. W., Moffat, S. D., Wiener, J. M., Barnes, C. A., & Wolbers, T. (2017). The aging navigational system. *Neuron*, *95*(5), 1019–1035. https://doi.org/10.1016/j.neuron.2017.06.037

Lich, M., & Bremmer, F. (2014). Self-motion perception in the elderly. *Frontiers in Human Neuroscience*, *8*, 1–15. https://doi.org/10.3389/fnhum.2014.00681

Lithfous, S., Dufour, A., Bouix, C., Pebayle, T., & Després, O. (2018). Reduced parahippocampal theta activity during spatial navigation in low, but not in high elderly performers. *Neuropsychology*, *32*(1), 40–53. https://doi.org/10.1037/neu0000392

Lithfous, S., Tromp, D., Dufour, A., Pebayle, T., Goutagny, R., & Després, O. (2015). Decreased theta power at encoding and cognitive mapping deficits in elderly individuals during a spatial memory task. *Neurobiology of Aging*, *36*(10), 2821–2829. https://doi.org/10.1016/j.neurobiolaging.2015.07.007

Logothetis, N. K., Eschenko, O., Murayama, Y., Augath, M., Steudel, T., Evrard, H. C., … Oeltermann, A. (2012). Hippocampal–cortical interaction during periods of subcortical silence. *Nature*, *491*(7425), 547–553. https://doi.org/10.1038/nature11618

Lubec, J., Smidak, R., Malikovic, J., Feyissa, D. D., Korz, V., Höger, H., & Lubec, G. (2019). Dentate gyrus peroxiredoxin 6 levels discriminate aged unimpaired from impaired rats in a spatial memory task. *Frontiers in Aging Neuroscience*, *10*(198), 1–11. https://doi.org/10.3389/fnagi.2019.00198

Lupien, S. J., Evans, A., Lord, C., Miles, J., Pruessner, M., Pike, B., & Pruessner, J. C. (2007). Hippocampal volume is as variable in young as in older adults: Implications for the notion of hippocampal atrophy in humans. *Neuroimage*, *34*(2), 479–485. https://doi.org/10.1016/j.neuroimage.2006.09.041

McQuail, J. A., Beas, B. S., Kelly, K. B., Simpson, K. L., Frazier, C. J., Setlow, B., & Bizon, J. L. (2016). NR2A-containing NMDARs in the prefrontal cortex are required for working memory and associated with age-related cognitive decline. *Journal of Neuroscience*, *36*(50), 12537–12548. https://doi.org/10.1523/JNEUROSCI.2332-16.2016

Ménard, C., Quirion, R., Vigneault, E., Bouchard, S., Ferland, G., El Mestikawy, S., & Gaudreau, P. (2015). Glutamate presynaptic vesicular transporter and postsynaptic receptor levels correlate with spatial memory status in aging rat models. *Neurobiology of Aging*, *36*(3), 1471–1482. https://doi.org/10.1016/j.neurobiolaging.2014.11.013

Merhav, M., & Wolbers, T. (2019). Aging and spatial cues influence the updating of navigational memories. *Scientific Reports*, *9*(1), 11469. https://doi.org/10.1038/s41598-019-47971-2

Moffat, S. D., Elkins, W., & Resnick, S. M. (2006). Age differences in the neural systems supporting human allocentric spatial navigation. *Neurobiology of Aging*, *27*(7), 965–972. https://doi.org/10.1016/j.neurobiolaging.2005.05.011

Moffat, S. D., Kennedy, K. M., Rodrigue, K. M., & Raz, N. (2007). Extrahippocampal contributions to age differences in human spatial navigation. *Cerebral Cortex*, *17*(6), 1274–1282. https://doi.org/10.1093/cercor/bhl036

Moffat, S. D., & Resnick, S. M. (2002). Effects of age on virtual environment place navigation and allocentric cognitive mapping. *Behavioral Neuroscience*, *116*(5), 851–859. https://doi.org/10.1037/0735-7044.116.5.851

Moser, M. B., Rowland, D. C., & Moser, E. I. (2015). Place cells, grid cells, and memory. *Cold Spring Harbor Perspectives in Biology*, *7*(2), a021808. https://doi.org/10.1101/cshperspect.a021808

Muehlroth, B. E., & Werkle-Bergner, M. (2020). Understanding the interplay of sleep and aging: Methodological challenges. *Psychophysiology*, *57*(3), e13523. https://doi.org/10.1111/psyp.13523

Negrón-Oyarzo, I., Espinosa, N., Aguilar-Rivera, M., Fuenzalida, M., Aboitiz, F., & Fuentealba, P. (2018). Coordinated prefrontal–hippocampal activity and navigation strategy-related prefrontal firing during spatial memory formation. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(27), 7123–7128.

Neves, G., Cooke, S. F., & Bliss, T. V. P. (2008). Synaptic plasticity, memory and the hippocampus: A neural network approach to causality. *Nature Reviews Neuroscience*, *9*(1), 65–75. https://doi.org/10.1038/nrn2303

Nyberg, L., Salami, A., Andersson, M., Eriksson, J., Kalpouzos, G., Kauppi, K., … Nilsson, L. G. (2010). Longitudinal evidence for diminished frontal cortex function in aging. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(52), 22682–22686. https://doi.org/10.1073/pnas.1012651108

Nyberg, L., Lövdén, M., Riklund, K., Lindenberger, U., & Bäckman, L. (2012). Memory aging and brain maintenance. *Trends in Cognitive Sciences*, *16*(5), 292–305. https://doi.org/10.1016/j.tics.2012.04.005

Nyberg, L., & Pudas, S. (2019). Successful memory aging. *Annual Review of Psychology*, *70*, 219–243. https://doi.org/10.1146/annurev-psych-010418-103052

Ólafsdóttir, H. F., Bush, D., & Barry, C. (2018). The role of hippocampal replay in memory and planning. *Current Biology*, *28*(1), R37–R50. https://doi.org/10.1016/j.cub.2017.10.073

Olsen, R. K., Yeung, L. K., Noly-Gandon, A., D'Angelo, M. C., Kacollja, A., Smith, V. M., … Barense, M. D. (2017). Human anterolateral entorhinal cortex volumes are associated with cognitive decline in aging prior to clinical diagnosis. *Neurobiology of Aging*, *57*, 195–205. https://doi.org/10.1016/J.NEUROBIOLAGING.2017.04.025

Palermo, L., Iaria, G., & Guariglia, C. (2008). Mental imagery skills and topographical orientation in humans: A correlation study. *Behavioural Brain Research*, *192*(2), 248–253. https://doi.org/10.1016/j.bbr.2008.04.014

Pascual, M. G., Zhang, L., Defelipe, J., Gaser, C., Medina, M., & Strange, B. A. (2020). Neuroanatomical signature of super-ageing: Structural brain study of youthful episodic memory in people over the age of 80. *Alzheimer's & Dementia*, *16*(S4), e041915. https://doi.org/10.1002/alz.041915

Persson, J., Kalpouzos, G., Nilsson, L.-G., Ryberg, M., & Nyberg, L. (2011). Preserved hippocampus activation in normal aging as revealed by fMRI. *Hippocampus*, *21*(7), 753–766. https://doi.org/10.1002/hipo.20794

Pu, Y., Cornwell, B. R., Cheyne, D., & Johnson, B. W. (2017). The functional role of human right hippocampal/parahippocampal theta rhythm in environmental encoding during virtual spatial navigation. *Human Brain Mapping*, *38*(3), 1347–1361. https://doi.org/10.1002/hbm.23458

Ramanoël, S., York, E., Le Petit, M., Lagrené, K., Habas, C., & Arleo, A. (2019). Age-related differences in functional and structural connectivity in the spatial navigation brain network. *Frontiers in Neural Circuits*, *13*, 1–13. https://doi.org/10.3389/fncir.2019.00069

Ramkhalawansingh, R., Keshavarz, B., Haycock, B., Shahab, S., & Campos, J. L. (2017). Examining the effect of age on visual–vestibular self-motion perception using a driving paradigm. *Perception*, *46*(5), 566–585. https://doi.org/10.1177/0301006616675883

Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., … Acker, J. D. (2005). Regional brain changes in aging healthy adults: General trends, individual differences and modifiers. *Cerebral Cortex*, *15*(11), 1676–1689. https://doi.org/10.1093/cercor/bhi044

Reagh, Z. M., Ho, H. D., Leal, S. L., Noche, J. A., Chun, A., Murray, E. A., & Yassa, M. A. (2016). Greater loss of object than spatial mnemonic discrimination in aged adults. *Hippocampus*, *26*(4), 417–422. https://doi.org/10.1002/hipo.22562

Reagh, Z. M., & Yassa, M. A. (2014). Object and spatial mnemonic interference differentially engage lateral and medial entorhinal cortex in humans. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(40), E4264–E4273. https://doi.org/10.1073/pnas.1411250111

Reagh, Z., & Yassa, M. (2017). Selective vulnerabilities and biomarkers in neurocognitive aging. *F1000Research*, *6*, 491. https://doi.org/10.12688/f1000research.10652.1

Reynolds, N. C., Zhong, J. Y., Clendinen, C. A., Moffat, S. D., & Magnusson, K. R. (2019). Age-related differences in brain activations during spatial memory formation in a well-learned virtual Morris water maze (vMWM) task. *Neuroimage*, *202*, 116069. https://doi.org/10.1016/j.neuroimage.2019.116069

Richmond, L. L., Sargent, J. Q., Flores, S., & Zacks, J. M. (2018). Age differences in spatial memory for mediated environments. *Psychology and Aging*, *33*(6), 892–903. https://doi.org/10.1037/pag0000286

Rieckmann, A., Karlsson, S., Karlsson, P., Brehmer, Y., Fischer, H., Farde, L., … Bäckman, L. (2011). Dopamine D1 receptor associations within and between dopaminergic pathways in younger and elderly adults: Links to cognitive performance. *Cerebral Cortex*, *21*(9), 2023–2032. https://doi.org/10.1093/cercor/bhq266

Robin, J., Hirshhorn, M., Rosenbaum, R. S., Winocur, G., Moscovitch, M., & Grady, C. L. (2015). Functional connectivity of hippocampal and prefrontal networks during episodic and spatial memory based on real-world environments. *Hippocampus*, *25*(1), 81–93. https://doi.org/10.1002/hipo.22352

Rodgers, M. K., Sindone, J. A., & Moffat, S. D. (2012). Effects of age on navigation strategy. *Neurobiology of Aging*, *33*(1), 202.e15–202.e22. https://doi.org/10.1016/j.neurobiolaging.2010.07.021

Rogalski, E. J., Gefen, T., Shi, J., Samimi, M., Bigio, E., Weintraub, S., … Mesulam Marsel, M. (2013). Youthful memory capacity in old brains: Anatomic and genetic clues from the Northwestern SuperAging Project. *Journal of Cognitive Neuroscience*, *25*(1), 29–36. https://doi.org/10.1162/jocn_a_00300

Rogalski, E., Gefen, T., Mao, Q., Connelly, M., Weintraub, S., Geula, C., … Mesulam, M. M. (2019). Cognitive trajectories and spectrum of neuropathology in SuperAgers: The first 10 cases. *Hippocampus*, *29*(5), 458–467. https://doi.org/10.1002/hipo.22828

Rueckemann, J. W., Sosa, M., Giocomo, L. M., & Buffalo, E. A. (2021). The grid code for ordered experience. *Nature Reviews Neuroscience*, *22*(10), 637–649. https://doi.org/10.1038/s41583-021-00499-9

Schaaf, M. J. M., Workel, J. O., Lesscher, H. M., Vreugdenhil, E., Oitzl, M. S., & Kloet Ron, de, E. (2001). Correlation between hippocampal BDNF mRNA expression and memory performance in senescent rats. *Brain Research*, *915*(2), 227–233. https://doi.org/10.1016/S0006-8993(01)02855-4

Shing, Y. L., Werkle-Bergner, M., Brehmer, Y., Müller, V., Li, S. C., & Lindenberger, U. (2010). Episodic memory across the lifespan: The contributions of associative and strategic components. *Neuroscience & Biobehavioral Reviews*, *34*(7), 1080–1091. https://doi.org/10.1016/J.NEUBIOREV.2009.11.002

Shing, Y. L., Werkle-Bergner, M., Li, S. C., & Lindenberger, U. (2008). Associative and strategic components of episodic memory: A life-span dissociation. *Journal of Experimental Psychology: General*, *137*(3), 495–513. https://doi.org/10.1037/0096-3445.137.3.495

Shrager, Y., Kirwan, C. B., & Squire, L. R. (2008). Neural basis of the cognitive map: Path integration does not require hippocampus or entorhinal cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(33), 12034–12038. https://doi.org/10.1073/pnas.0805414105

Spiers, H. J. (2008). Keeping the goal in mind: Prefrontal contributions to spatial navigation. *Neuropsychologia*, *46*(7), 2106–2108. https://doi.org/10.1016/j.neuropsychologia.2008.01.028

Stangl, M., Achtzehn, J., Huber, K., Dietrich, C., Tempelmann, C., & Wolbers, T. (2018). Compromised grid-cell-like representations in old age as a key mechanism to explain age-related navigational deficits. *Current Biology*, *28*(7), 1108–1115.e6. https://doi.org/10.1016/j.cub.2018.02.038

Stangl, M., Kanitscheider, I., Riemer, M., Fiete, I., & Wolbers, T. (2020). Sources of path integration error in young and aging humans. *Nature Communications*, *11*(1), 2626. https://doi.org/10.1038/s41467-020-15805-9

Storsve, A. B., Fjell, A. M., Tamnes, C. K., Westlye, L. T., Overbye, K., Aasland, H. W., & Walhovd, K. B. (2014). Differential longitudinal changes in cortical thickness, surface area and volume across the adult life span: Regions of accelerating and decelerating change. *Journal of Neuroscience*, *34*(25), 8488–8498. https://doi.org/10.1523/JNEUROSCI.0391-14.2014

Stranahan, A. M., & Mattson, M. P. (2010). Selective vulnerability of neurons in layer II of the entorhinal cortex during aging and Alzheimer's disease. *Neural Plasticity*, *2010*, 108190. https://doi.org/10.1155/2010/108190

Sugar, J., & Moser, M. B. (2019). Episodic memory: Neuronal codes for what, where, and when. *Hippocampus*, *29*(12), 1190–1205. https://doi.org/10.1002/hipo.23132

Takeuchi, T., Duszkiewicz, A. J., & Morris, R. G. M. (2014). The synaptic plasticity and memory hypothesis: Encoding, storage and persistence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *369*(1633), 20130288. https://doi.org/10.1098/rstb.2013.0288

Thomé, A., Gray, D. T., Erickson, C. A., Lipa, P., & Barnes, C. A. (2016). Memory impairment in aged primates is associated with region-specific network dysfunction. *Molecular Psychiatry*, *21*(9), 1257–1262. https://doi.org/10.1038/mp.2015.160

Tromp, D., Dufour, A., Lithfous, S., Pebayle, T., & Després, O. (2015). Episodic memory in normal aging and Alzheimer disease: Insights from imaging and behavioral studies. *Ageing Research Reviews*, *24*, 232–262. https://doi.org/10.1016/j.arr.2015.08.006

Tulving, E. (2002). Episodic memory: From mind to brain. *Annual Review of Psychology*, *53*, 1–25. https://doi.org/10.1146/annurev.psych.53.100901.135114

Van der Ham, I. J. M., Claessen, M. H. G., Evers, A. W. M., & van der Kuil, M. N. A. (2020). Large-scale assessment of human navigation ability across the lifespan. *Scientific Reports*, *10*(1), 3299. https://doi.org/10.1038/s41598-020-60302-0

Van Strien, N. M., Cappaert, N. L. M., & Witter, M. P. (2009). The anatomy of memory: An interactive overview of the parahippocampal-hippocampal network. *Nature Reviews. Neuroscience*, *10*(4), 272–282. https://doi.org/10.1038/NRN2614

Vanhaute, H., Ceccarini, J., Michiels, L., Sunaert, S., Lemmens, R., Emsell, L., … Van Laere, K. (2019). *Changes in synaptic density in relation to tau deposition in prodromal Alzheimer's disease: A dual protocol {PET}-{MR} study.*

Varga, A. W., Ducca, E. L., Kishi, A., Fischer, E., Parekh, A., Koushyk, V., … Ayappa, I. (2016). Effects of aging on slow-wave sleep dynamics and human spatial navigational memory consolidation. *Neurobiology of Aging*, *42*, 142–149. https://doi.org/10.1016/j.neurobiolaging.2016.03.008

Wang, R. F. (2016). Building a cognitive map by assembling multiple path integration systems. *Psychonomic Bulletin and Review*, *23*(3), 692–702. https://doi.org/10.3758/s13423-015-095

Wanjia, G., Favila, S. E., Kim, G., Molitor, R. J., & Kuhl, B. A. (2021). Abrupt hippocampal remapping signals resolution of memory interference. *Nature Communications*, *12*(1), 4816. https://doi.org/10.1038/s41467-021-25126-0

Watrous, A. J., Fried, I., & Ekstrom, A. D. (2011). Behavioral correlates of human hippocampal delta and theta oscillations during navigation. *Journal of Neurophysiology*, *105*(4), 1747–1755. https://doi.org/10.1152/jn.00921.2010

Wiegand, J. P., Gray, D. T., Schimanski, L. A., Lipa, P., Barnes, C. A., & Cowen, S. L. (2016). Age is associated with reduced sharp-wave ripple frequency and altered patterns of neuronal variability. *Journal of Neuroscience*, *36*(20), 5650–5660. https://doi.org/10.1523/JNEUROSCI.3069-15.2016

Wiener, J. M., de Condappa, O., Harris, M. A., & Wolbers, T. (2013). Maladaptive bias for extrahippocampal navigation strategies in aging humans. *Journal of Neuroscience*, *33*(14), 6012–6017. https://doi.org/10.1523/JNEUROSCI.0717-12.2013

Wiener, J. M., Kmecova, H., & de Condappa, O. (2012). Route repetition and route retracing: Effects of cognitive aging. *Frontiers in Aging Neuroscience*, *4*(7), 1–7. https://doi.org/10.3389/fnagi.2012.00007

Yamamoto, N., & DeGirolamo, G. J. (2012). Differential effects of aging on spatial learning through exploratory navigation and map reading. *Frontiers in Aging Neuroscience*, *4*(14), 1–7. https://doi.org/10.3389/fnagi.2012.00014

Yang, S., Megill, A., Ardiles, A. O., Ransom, S., Tran, T., Koh, M. T., … Kirkwood, A. (2013). Integrity of mGluR-LTD in the associative/commissural inputs to CA3 correlates with successful aging in rats. *Journal of Neuroscience*, *33*(31), 12670–12678. https://doi.org/10.1523/JNEUROSCI.1086-13.2013

Yeung, L. K., Olsen, R. K., Hong, B., Mihajlovic, V., D'angelo, M. C., Kacollja, A., … Barense, M. D. (2019). Object-in-place memory predicted by anterolateral entorhinal cortex and parahippocampal cortex volume in older adults. *Journal of Cognitive Neuroscience*, *31*(5), 711–729. https://doi.org/10.1162/JOCN_A_01385

Zhong, J. Y., Magnusson, K. R., Swarts, M. E., Clendinen, C. A., Reynolds, N. C., & Moffat, S. D. (2017). The application of a rodent-based Morris water maze (MWM) protocol to an investigation of age-related differences in human spatial learning. *Behavioral Neuroscience*, *131*(6), 470–482. https://doi.org/10.1037/bne0000219

Zhong, J. Y., & Moffat, S. D. (2018). Extrahippocampal contributions to age-related changes in spatial navigation ability. *Frontiers in Human Neuroscience*, *12*, 272. https://doi.org/10.3389/fnhum.2018.00272