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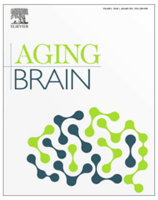

Future trends in brain aging research: Visuo-cognitive functions at stake during mobility and spatial navigation

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ABSTRACT

Aging leads to a complex pattern of structural and functional changes, gradually affecting sensorimotor, perceptual, and cognitive processes. These multiscale changes can hinder older adults' interaction with their environment, progressively reducing their autonomy in performing tasks relevant to everyday life. Autonomy loss can further be aggravated by the onset and progression of neurodegenerative disorders (e.g., age-related macular degeneration at the sensory input level; and Alzheimer's disease at the cognitive level). In this context, spatial cognition offers a representative case of high-level brain function that involves multimodal sensory processing, postural control, locomotion, spatial orientation, and wayfinding capabilities. Hence, studying spatial behavior and its neural bases can help identify early markers of pathogenic age-related processes. Until now, the neural correlates of spatial cognition have mostly been studied in static conditions thereby disregarding perceptual (other than visual) and motor aspects of natural navigation. In this review, we first demonstrate how visuo-motor integration and the allocation of cognitive resources during locomotion lie at the heart of real-world spatial navigation. Second, we present how technological advances such as immersive virtual reality and mobile neuroimaging solutions can enable researchers to explore the interplay between perception and action. Finally, we argue that the future of brain aging research in spatial navigation demands a widespread shift toward the use of naturalistic, ecologically valid experimental paradigms to address the challenges of mobility and autonomy decline across the lifespan.

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Healthy aging is characterized by heterogeneous modifications that affect perceptual, cognitive, and motor functions [48]. Spatial navigation, a fundamental daily ability that requires the integration of multimodal information, is known to decline across the life span [32]. An extensive body of literature reports age-related impairments in navigational skills such as difficulty with learning new routes, reorienting, and estimating distances [35,39,53]. A consequence of these spatial navigation deficits is that older adults see a decline in their mobility and autonomy, resulting in an increased risk of progression of age-related neurodegenerative disorders such as Alzheimer's disease [19]. Hence, investigating spatial navigation in the older adult population could have far-reaching implications for societies and individuals. For this reason, it is important to consider both the behavioral and neurobiological factors responsible for the deterioration of visuo-spatial functions

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throughout aging. A limited number of magnetic resonance imaging (MRI) studies have investigated the neural bases of spatial behavior in the context of healthy aging [33]. Findings often pertain to structural and functional age-related modifications in the hippocampus and other medial temporal structures, and a few highlight the possible implications of prefrontal, cerebellar, and occipital areas. Recent studies have indeed underlined age-related differences in the activity of early visual and visuo-spatial brain regions that appear to be associated with declining directional processing and spatial abilities [28,46]. From these results emerges the possibility that altered visual processing contributes significantly to spatial navigation deficits in aging. This hypothesis is in line with accumulating literature showing that visual impairments in older adults are a significant risk factor for cognitive decline [54]. The widespread use of structural and functional MRI has nonetheless hindered the possibility of considering spatial navigation in its entirety because perceptual (other than visual) and motor aspects are omitted. To address the latter caveats, a critical next step for obtaining a more accurate characterization of human brain aging is to take into account the multimodal nature of spatial navigation by designing studies that encompass multiple perceptual, locomotor, and cognitive factors.

Although, as humans, we rely extensively on vision, other types of sensory information, such as auditory, vestibular, and proprioceptive, are all at play during navigation [5]. Critically, the perceptual information available during navigation differentially modulates young and older adults' behavior. In young adults, several studies have reported similar performance during path integration (i.e., the capacity to keep track of one's position on a trajectory through the integration of rotational and translational displacements provided by self-motion cues) when participants relied on visual optic flow only, vestibular inertial information only, or vestibular and proprioceptive afferents conjointly [1,36,56]. In contrast, in older adults, the variety of sensory information available is known to determine their navigational performance [24,36]. Some age-related navigational deficits frequently observed in desktop-based tasks appear to be mitigated in mobile conditions (virtual reality and real-world settings), which highlights the importance of the availability of multimodal information to improve navigational performance in older adults [27,38]. These findings emphasize that multisensory integration can at least partially alleviate certain struggles faced by older adults when navigating, by compensating for age-related unisensory degradations [7]. Thus, shedding light on specific facilitative and competitive mechanisms between sensory inputs can help refine our understanding of navigation performance maintenance and decline as people age.

Postural control and locomotion represent essential aspects of spatial navigation that are frequently neglected by brain aging studies. From a perceptual-motor perspective, the upweighting of visual cues and increased visual field dependence in older adults can have a drastic impact on their locomotor behavior and stability [3]. Evidence also suggests an important role for visuo-podal integration in postural control and mobility [18,47]. Strengthening the argument for close ties between visual and locomotor systems, an increasing number of rodent neurobiological studies suggest that visual brain patterns are modulated by motion-related inputs [44]. Motor-related skills are also tightly intertwined with the attentional and cognitive factors that lie at the heart of spatial navigation. In older adults, attentional resources are neither precisely nor optimally allocated in situations that require intricate multitasking capabilities, such as when performing two motor actions simultaneously [52]. During spatial navigation, the attentional resources dedicated to postural control and locomotion can even interfere with the other cognitive processes at play [2,26]. Most strikingly, age-related deficits in balance and locomotion induce an increased fear of falling that in turn shapes older adults' navigable space and it forces them to adapt their walking behavior. Indeed, older navigators tend to walk more slowly, to focus their gaze on the ground, and to avoid obstacles in their peripersonal space. These age-related changes could contribute to suboptimal spatial learning and orientation in older adults. For example, older adults place emphasis on body awareness and stability when walking rather than on the formation of a mental map to orient themselves in the immediate environment [58]. Beyond behavioral observations, neuroimaging findings show that age-related reductions in walking speed and increases in gait variability are linked to structural and functional changes in a distributed brain network encompassing prefrontal, frontal, parietal, occipital, cingulate, and thalamic regions [2,51,55]. Although it is striking that the neural underpinnings of age-related locomotor deficits widely overlap with those of spatial navigation [33,39,59], no study has yet tested these abilities concomitantly in older adults.

The interplay between sensory (in particular, visual), motor, and cognitive processes at stake during spatial navigation makes it necessary to use holistic approaches to conduct brain aging research. It is key to consider the full scope of behavioral and neural changes occurring across the life span. In this review article, we argue that studying the neural underpinnings of visuo-spatial information processing in aging also requires a shift toward more ecologically valid experimental paradigms, which leverage the recent technological advances in both virtual reality (VR) and mobile brain imaging.

One of the most notable technological innovations pertains to the development of increasingly reliable and affordable immersive VR devices. Commercial head-mounted displays now provide a precise coordination of the visual display, with head movements of the participant, thus enabling a near-naturalistic visuo-vestibular integration. The great advantage of VR over real-world setups lies in the high level of control of all environmental variables that it offers. Indeed, environments can be designed so they perfectly fit with the experimental task, and relevant parameters can be varied systematically. In parallel, great progress has been made in rendering the recording of various biomarkers feasible in mobile conditions. The most important recording techniques in the field of navigation are mobile eye-tracking and motion capture. Accessing the oculomotor behavior of participants can be informative when striving to uncover navigationally relevant information, visual exploration strategies, or movement planning [8]. Similarly, motion capture allows for the investigation of body movements and gait metrics such as walking speed and trajectory efficiency during navigation [2]. These technological improvements could considerably enrich the monitoring and thus the understanding of aging spatial behavior in near-naturalistic conditions. Commercial VR setups are still facing several limitations and challenges, such as a reduced field of view and the presence of incongruences between visual and motor inputs (for a review, see [15]). New devices are already closing the gap with a more natural human field of view and motion-to-image latencies that are becoming undetectable to human perception.

In parallel to VR and motion capture technologies, the development of brain recording techniques in moving humans opens up new and exciting research perspectives. To date, several brain imaging systems have been tested and adopted in mobile conditions: scalp electroencephalography (EEG; [20]), functional near-infrared spectroscopy (fNIRS; [6]), and intracranial electroencephalography (iEEG; [4]). Because of the required surgical intervention, iEEG cannot be considered for systematic use in healthy participants, and it remains constrained to the chemically resistant epileptic population. In contrast, the accessible and noninvasive natures of EEG and fNIRS make them ideal candidates for recording large samples of subjects across the life span. EEG has drawn more interest, and it has developed more rapidly than fNIRS for imaging in mobile conditions because it offers a sub-second timescale window into the dynamics of cognitive processes. Thus, in this review article, we will focus on mobile EEG, which provides a large majority of the supporting evidence discussed within the scope of this article (for a more thorough review, see [42]). Major technical obstacles related to recording brain signals in motion have recently been overcome. For example, the sensitivity of EEG to artifacts in mobile conditions has been mitigated through the development of active electrodes and cable shielding [31]. Lighter amplifiers and wireless capabilities have enabled new systems to record high-quality data without tying the subject to a desktop [41]. More importantly, advances in data-processing methods have advantageously been applied to EEG recordings to detect and remove the aforementioned artifacts. Blind source separation algorithms such as independent component analysis have proven useful in isolating artifactual components from neural signals [14], even in the case of mobile EEG data [23]. Blind source separation also facilitates solving of the EEG inverse problem (i.e., finding the spatial origin of the EEG signal of interest). Leveraging these advances, the mobile brain and body imaging (MoBI) approach [21] has now gained enough momentum to provide interesting opportunities for brain aging research. In particular, the co-registration of brain signals and biometric measures like body and eye movements allows neuroscientists to design mobile experiments that unlock new dimensions of brain signal interpretation.

Several research groups have started combining the above-mentioned methodologies and have shown that accounting for mobility is pivotal to fully understand the action-perception loop during spatial behavior. Regarding multisensory integration, Ehinger et al.'s [17] pioneering study demonstrated that brain rhythms were significantly modulated by the presence of natural vestibular and kinesthetic feedback during spatial orientation. This was recently replicated by Gramann et al. [22], who reported differences in EEG activity from the retrosplenial complex between stationary and full-body rotation setups. Their results suggest that a strong desynchronization in the alpha band could be a marker of a sensory mismatch between vision and proprioception during full-body rotations. The latter finding questions previous studies conducted in static conditions that linked this alpha desynchronization with heading computation. Mobile neuroimaging studies have also started to unriddle the complex interaction between visual processing, cognition, and locomotion at the neural level. Cao and Händel [12] showed that EEG-recorded alpha oscillations during walking reflected increased processing of peripheral visual inputs. The current locomotion state of the body was also found to affect eye movement patterns; taken together, these results reflect an underlying strategy of optimizing the extraction of sensory information during locomotion [11]. With respect to cognitive factors required during locomotion, Ladouce et al. [30] recently employed mobile EEG to understand how participants allocate cognitive resources when tasked with identifying visual targets in moving conditions. They found that the additional cognitive demands during movement reduced the attention of participants to the stimuli of interest, as reflected by the event-related potential P300. Similarly, in a study including both young and older adults, Protzak et al. [45] identified the neural markers associated with worsened visual processing during ambulation that were more pronounced in older adults. The latter results bring into focus the importance of understanding how, on both behavioral and neural levels, attention is reallocated to perceptual, cognitive, or motor processing in older adults during natural, active spatial behavior. Indeed, aging research has extensively used the MoBI framework to study cognitive-motor interference in older participants by using dual-task paradigms [9,10,25,37,45]. Finally, a growing number of mobile EEG studies are assessing more fundamental scientific hypotheses related to spatial learning, representation, or memory (e.g., [34,43,50]), perception of obstacles and affordances [16,40], and landmark-based spatial navigation [13,57].

We believe that applying the paradigm shift discussed so far to an even wider range of scientific questions would significantly benefit aging research. First, understanding how older adults process and use information to move about in large and complex environments (e.g., train stations or shopping centers) could lead to important changes in urban planning. Could we facilitate spatial learning by providing additional sensory cues and by lowering cognitive-motor demands (e.g., flat terrain, fewer stairs)? Should we rethink the size and position of signage in stations? Second, the neuroimaging of spatial navigation in mobile conditions could prove to be a turning point in our comprehension of age-related navigation deficits. Going beyond the selective investigation of targeted brain regions with simple sensory stimulation, connectivity analyses of real-time interactions between several brain areas could change our current knowledge of spatial cognition. How could the interaction and the fine-grained time course between sensory and motor signals modify cognitive processing in the navigation network? Could the presence of specific sensory and motor signals refine the visual input and thus mitigate spatial learning difficulties in older adults? Such studies would, by extension, shed light on the etiology of neurodegenerative diseases in which spatial navigation can deteriorate dramatically, as is the case in Mild Cognitive Impairment and Alzheimer's disease [29,49]. Third, pinpointing the individual contribution of sensory, cognitive, and motor processes in real-life navigational scenarios could be particularly beneficial to the development of rehabilitation protocols or targeted medical devices for age-related visual pathologies. For example, portable neuroimaging devices could be used for real-time neurofeedback to reweigh reliance on specific visual or proprioceptive information during locomotion.

We conclude that the study of brain aging in mobile, naturalistic conditions provides a novel framework to study the multiscale factors at stake during locomotion and spatial orientation in older adults. It would also allow behavioral and neural biomarkers to be identified to differentiate healthy from pathological aging trajectories.

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