



**HAL**  
open science

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

Stephen Ramanoël, Marion Durteste, Alexandre Delaux, Jean-Baptiste de Saint Aubert, Angelo Arleo

### ► **To cite this version:**

Stephen Ramanoël, Marion Durteste, Alexandre Delaux, Jean-Baptiste de Saint Aubert, Angelo Arleo. Future trends in brain aging research: Visuo-cognitive functions at stake during mobility and spatial navigation. *Aging Brain*, 2022, 2, pp.100034. 10.1016/j.nbas.2022.100034 . hal-03793985

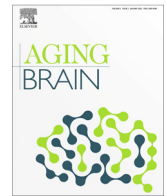
**HAL Id: hal-03793985**

**<https://hal.sorbonne-universite.fr/hal-03793985>**

Submitted on 2 Oct 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



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

Stephen Ramanoël<sup>a,b</sup>, Marion Durteste<sup>a</sup>, Alexandre Delaux<sup>a</sup>, Jean-Baptiste de Saint Aubert<sup>a</sup>, Angelo Arleo<sup>a,\*</sup>

<sup>a</sup>Sorbonne Université, INSERM, CNRS, Institut de la Vision, 17 rue Moreau, F-75012 Paris, France

<sup>b</sup>Université Côte d'Azur, LAMHESS, Nice, France

### ARTICLE INFO

#### Article history:

Received 19 January 2022

Revised 31 January 2022

Accepted 2 February 2022

#### Keywords:

Visual aging

Cognitive aging

Spatial navigation

Mobile neuroimaging

### 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.

© 2022 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

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

\* Corresponding author.

E-mail address: [angelo.arleo@inserm.fr](mailto:angelo.arleo@inserm.fr) (A. Arleo).

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 multi-tasking 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 rele-

vant 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 time-scale 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.

## Funding

This research was supported by the Chair SILVERSIGHT Agence Nationale de la Recherche (ANR-18-CHIN-0002), the LabEx LIFESENSES (ANR-10-LABX-65), the IHU FORESIGHT (ANR-18-IAHU-01), and the Fondation pour la Recherche sur Alzheimer (FRA).

## References

- Adamo DE, Briceno EM, Sindone JA, Alexander NB, Moffat SD. Age differences in virtual environment and real world path integration. *Front Aging Neurosci* 2012;4:26. doi: <https://doi.org/10.3389/fnagi.2012.00026>.
- Agathos CP, Ramanoël S, Bécu M, Bernardin D, Habas C, Arleo A. Postural Control While Walking Interferes With Spatial Learning in Older Adults Navigating in a Real Environment. *Front Aging Neurosci* 2020;12:. doi: <https://doi.org/10.3389/fnagi.2020.588653>.
- Agathos CP, Bernardin D, Huchet D, Scherlen AC, Assaïante C, Isableu B. Sensorimotor and cognitive factors associated with the age-related increase of visual field dependence: a cross-sectional study. *AGE* 2015;37:67. doi: <https://doi.org/10.1007/s11357-015-9805-x>.
- Aghajan ZM, Schuette P, Fields TA, Tran ME, Siddiqui SM, Hasulak NR, et al. Theta Oscillations in the Human Medial Temporal Lobe during Real-World Ambulatory Movement. *Curr Biol* 2017;27(24):3743–3751.e3. doi: <https://doi.org/10.1016/j.cub.2017.10.062>.
- Arleo Angelo, Rondi-reig Laure. Multimodal sensory integration and concurrent navigation strategies for spatial cognition in real and artificial organisms. *J Integr Neurosci* 2007;06(03):327–66.
- Atsumori H, Kiguchi M, Katura T, Funane T, Obata A, Sato H, et al. Noninvasive imaging of prefrontal activation during attention-demanding tasks performed while walking using a wearable optical topography system. *J Biomed Opt* 2010;15:. doi: <https://doi.org/10.1117/1.3462996>.
- Bates SL, Wolbers T. How cognitive aging affects multisensory integration of navigational cues. *Neurobiol Aging* 2014;35(12):2761–9. doi: <https://doi.org/10.1016/j.neurobiolaging.2014.04.003>.
- Bécu M, Sheynikhovich D, Tatur G, Agathos CP, Bologna LL, Sahel J-A, et al. Age-related preference for geometric spatial cues during real-world navigation. *Nat Hum Behav* 2020;4(1):88–99. doi: <https://doi.org/10.1038/s41562-019-0718-z>.
- Beurskens R, Helmich J, Rein R, Bock O. Age-related changes in prefrontal activity during walking in dual-task situations: A fNIRS study. *Int J Psychophysiol* 2014;92(3):122–8. doi: <https://doi.org/10.1016/j.ijpsycho.2014.03.005>.
- Bohle H, Rimpel J, Schauenburg G, Gebel A, Stelzel C, Heinzl S, et al. Behavioral and Neural Correlates of Cognitive-Motor Interference during Multitasking in Young and Old Adults. *Neural Plasticity* 2019;2019:1–19. doi: <https://doi.org/10.1155/2019/9478656>.
- Cao L, Chen X, Haendel BF. Overground Walking Decreases Alpha Activity and Entrain Eye Movements in Humans. *Front Hum Neurosci* 2020;14:. doi: <https://doi.org/10.3389/fnhum.2020.561755>.
- Cao L, Händel B, Pack CC. Walking enhances peripheral visual processing in humans. *PLoS Biol* 2019;17(10):e3000511. doi: <https://doi.org/10.1371/journal.pbio.3000511>.
- Delaux A, Saint Aubert J-B, Ramanoël S, Bécu M, Gehrke L, Klug M, et al. Mobile brain/body imaging of landmark-based navigation with high-density EEG. *Eur J Neurosci* 2021;54(12):8256–82. doi: <https://doi.org/10.1111/ejn.15190>.
- Delorme A, Sejnowski T, Makeig S. Enhanced detection of artifacts in EEG data using higher-order statistics and independent component analysis. *NeuroImage* 2007;34(4):1443–9. doi: <https://doi.org/10.1016/j.neuroimage.2006.11.004>.
- Diersch N, Wolbers T. The potential of virtual reality for spatial navigation research across the adult lifespan. *J Exp Biol* 2019;222(Suppl\_1). doi: <https://doi.org/10.1242/jeb.187252>.
- Djebbara Z, Fich LB, Gramann K. The brain dynamics of architectural affordances during transition. *Sci Rep* 2021;11:2796. doi: <https://doi.org/10.1038/s41598-021-82504-w>.
- Ehinger BV, Fischer P, Gert AL, Kaufhold L, Weber F, Pipa G, et al. Kinesthetic and vestibular information modulate alpha activity during spatial navigation: a mobile EEG study. *Front Hum Neurosci* 2014;8:71. doi: <https://doi.org/10.3389/fnhum.2014.00071>.
- Foisy A, Kapoula Z. Plantar cutaneous afferents influence the perception of subjective visual vertical in quiet stance. *Sci Rep* 2018;8:14939. doi: <https://doi.org/10.1038/s41598-018-33268-3>.
- Gelfo F, Mandolesi L, Serra L, Sorrentino G, Caltagirone C. The Neuroprotective Effects of Experience on Cognitive Functions: Evidence from Animal Studies on the Neurobiological Bases of Brain Reserve. *Neuroscience* 2018;370:218–35. doi: <https://doi.org/10.1016/j.neuroscience.2017.07.065>.
- Gramann K, Gwin JT, Bigdely-Shamlo N, Ferris DP, Makeig S. Visual Evoked Responses During Standing and Walking. *Front Hum Neurosci* 2010;4:202. doi: <https://doi.org/10.3389/fnhum.2010.00202>.
- Gramann K, Gwin JT, Ferris DP, Oie K, Jung T-P, Lin C-T, et al. Cognition in action: imaging brain/body dynamics in mobile humans. *Rev Neurosci* 2011;22(6). doi: <https://doi.org/10.1515/RNS.2011.047>.
- Gramann K, Hohlefeld FU, Gehrke L, Klug M. Human cortical dynamics during full-body heading changes. *Sci Rep* 2021;11:18186. doi: <https://doi.org/10.1038/s41598-021-97749-8>.
- Gwin JT, Gramann K, Makeig S, Ferris DP. Removal of movement artifact from high-density EEG recorded during walking and running. *J Neurophysiol* 2010;103(6):3526–34. doi: <https://doi.org/10.1152/jn.00105.2010>.
- Harris MA, Wolbers T. Ageing effects on path integration and landmark navigation. *Hippocampus* 2012;22(8):1770–80. doi: <https://doi.org/10.1002/hipo.22011>.
- Holtzer R, Mahoney JR, Izzetoglu M, Wang C, England S, Verghese J. Online fronto-cortical control of simple and attention-demanding locomotion in humans. *NeuroImage* 2015;112:152–9. doi: <https://doi.org/10.1016/j.neuroimage.2015.03.002>.
- Holtzer R, Verghese J, Xue X, Lipton RB. Cognitive processes related to gait velocity: results from the einstein aging study. *Neuropsychology* 2006;20:215–23. doi: <https://doi.org/10.1037/0894-4105.20.2.215>.
- Kirasic KC. Spatial cognition and behavior in young and elderly adults: implications for learning new environments. *Psychol Aging* 1991;6(1):10–8. doi: <https://doi.org/10.1037/0882-7974.6.1.10>.
- Koch C, Li S-C, Polk TA, Schuck NW. Effects of aging on encoding of walking direction in the human brain. *Neuropsychologia* 2020;141:107379. doi: <https://doi.org/10.1016/j.neuropsychologia.2020.107379>.
- Laczó M, Wiener JM, Kalinova J, Matuskova V, Vyhnaek M, Hort J, et al. Spatial Navigation and Visuospatial Strategies in Typical and Atypical Aging. *Brain Sci* 2021;11(11):1421. doi: <https://doi.org/10.3390/brainsci11111421>.

- [30] Ladouce S, Donaldson DI, Dudchenko PA, Ietswaart M. Mobile EEG identifies the re-allocation of attention during real-world activity. *Sci Rep* 2019;9:15851. doi: <https://doi.org/10.1038/s41598-019-51996-y>.
- [31] Laszlo S, Ruiz-Blondet M, Khalifian N, Chu F, Jin Z. A direct comparison of active and passive amplification electrodes in the same amplifier system. *J Neurosci Methods* 2014;235:298–307. doi: <https://doi.org/10.1016/j.jneumeth.2014.05.012>.
- [32] Lester, A.W., Moffat, S.D., Wiener, J.M., Barnes, C.A., Wolbers, T. (2017) The Aging Navigational System. *Neuron*, 95,1019–1035. <https://doi.org/10.1016/j.neuron.2017.06.03>
- [33] Li AWY, King J. Spatial memory and navigation in ageing: A systematic review of MRI and fMRI studies in healthy participants. *Neurosci Biobehav Rev* 2019;103:33–49. doi: <https://doi.org/10.1016/j.neubiorev.2019.05.005>.
- [34] Liang M, Zheng J, Isham E, Ekstrom A. Common and Distinct Roles of Frontal Midline Theta and Occipital Alpha Oscillations in Coding Temporal Intervals and Spatial Distances. *J Cognit Neurosci* 2021;33:2311–27. doi: [https://doi.org/10.1162/jocn\\_a.01765](https://doi.org/10.1162/jocn_a.01765).
- [35] Lithfous S, Dufour A, Després O. Spatial navigation in normal aging and the prodromal stage of Alzheimer's disease: insights from imaging and behavioral studies. *Ageing Res Rev* 2013;12(1):201–13. doi: <https://doi.org/10.1016/j.arr.2012.04.007>.
- [36] Mahmood O, Adamo D, Briceno E, Moffat SD. Age differences in visual path integration. *Behav Brain Res* 2009;205(1):88–95. doi: <https://doi.org/10.1016/j.bbr.2009.08.001>.
- [37] Malcolm BR, Foxe JJ, Butler JS, De Sanctis P. The aging brain shows less flexible reallocation of cognitive resources during dual-task walking: A mobile brain/body imaging (MoBI) study. *Neuroimage* 2015;117:230–42. doi: <https://doi.org/10.1016/j.neuroimage.2015.05.028>.
- [38] McAvan AS, Du YK, Oyao A, Doner S, Grilli MD, Ekstrom A. Older Adults Show Reduced Spatial Precision but Preserved Strategy-Use During Spatial Navigation Involving Body-Based Cues. *Front Aging Neurosci* 2021;13. doi: <https://doi.org/10.3389/fnagi.2021.640188>.
- [39] Moffat SD. Aging and spatial navigation: What do we know and where do we go? *Neuropsychol Rev* 2009;19(4):478–89. doi: <https://doi.org/10.1007/s11065-009-9120-3>.
- [40] Mustile M, Kourtis D, Ladouce S, Learmonth G, Edwards MG, Donaldson DI, et al. Mobile EEG reveals functionally dissociable dynamic processes supporting real-world ambulatory obstacle avoidance: Evidence for early proactive control. *Eur J Neurosci* 2021;54(12):8106–19. doi: <https://doi.org/10.1111/ejn.15120>.
- [41] Oliveira AS, Schlink BR, Hairston WD, König P, Ferris DP. Proposing Metrics for Benchmarking Novel EEG Technologies Towards Real-World Measurements. *Front Hum Neurosci* 2016;10:188. doi: <https://doi.org/10.3389/fnhum.2016.00188>.
- [42] Park JL, Dudchenko PA, Donaldson DI. Navigation in Real-World Environments: New Opportunities Afforded by Advances in Mobile Brain Imaging. *Front Hum Neurosci* 2018;12:361. doi: <https://doi.org/10.3389/fnhum.2018.00361>.
- [43] Park JL, Donaldson DI. Detecting the neural correlates of episodic memory with mobile EEG: Recollecting objects in the real world. *Neuroimage* 2019;193:1–9. doi: <https://doi.org/10.1016/j.neuroimage.2019.03.013>.
- [44] Parker PRL, Brown MA, Smear MC, Niell CM. Movement-Related Signals in Sensory Areas: Roles in Natural Behavior. *Trends Neurosci* 2020;43(8):581–95. doi: <https://doi.org/10.1016/j.tins.2020.05.005>.
- [45] Protzak J, Wiczorek R, Gramann K. Peripheral visual perception during natural overground dual-task walking in older and younger adults. *Neurobiol Aging* 2021;98:146–59. doi: <https://doi.org/10.1016/j.neurobiolaging.2020.10.009>.
- [46] Ramanoël S, Durteste M, Bécu M, Habas C, Arleo A. Differential Brain Activity in Regions Linked to Visuospatial Processing During Landmark-Based Navigation in Young and Healthy Older Adults. *Front Hum Neurosci* 2020;14. doi: <https://doi.org/10.3389/fnhum.2020.552111>.
- [47] Roll R, Kavounoudias A, Roll J-P. Cutaneous afferents from human plantar sole contribute to body posture awareness. *NeuroReport* 2002;13(15):1957–61. doi: <https://doi.org/10.1097/00001756-2002-10280-00025>.
- [48] Salthouse TA. Trajectories of normal cognitive aging. *Psychol Aging* 2019;34:17–24. doi: <https://doi.org/10.1037/pag0000288>.
- [49] Segen V, Ying J, Morgan E, Brandon M, Wolbers T. Path integration in normal aging and Alzheimer's disease. *Trends Cognit Sci* 2022;26(2):142–58. doi: <https://doi.org/10.1016/j.tics.2021.11.001>.
- [50] Snider J, Plank M, Lynch G, Halgren E, Poizner H. Human Cortical during Free Exploration Encodes Space and Predicts Subsequent Memory. *J Neurosci* 2013;33:15056–68. doi: <https://doi.org/10.1523/JNEUROSCI.0268-13.2013>.
- [51] Tripathi S, Verghese J, Blumen HM. Gray matter volume covariance networks associated with dual-task cost during walking-while-talking. *Hum Brain Mapp* 2019;40(7):2229–40. doi: <https://doi.org/10.1002/hbm.24520>.
- [52] Tsang PS. Ageing and attentional control. *Q J Exp Psychol* 2013;66(8):1517–47. doi: <https://doi.org/10.1080/17470218.2012.752019>.
- [53] van der Ham IJM, Claessen MHG. How age relates to spatial navigation performance: Functional and methodological considerations. *Ageing Res Rev* 2020;58:101020. doi: <https://doi.org/10.1016/j.arr.2020.101020>.
- [54] Vu TA, Fenwick EK, Gan ATL, Man REK, Tan BKJ, Gupta P, et al. The Bidirectional Relationship between Vision and Cognition: A Systematic Review and Meta-analysis. *Ophthalmology* 2021;128(7):981–92. doi: <https://doi.org/10.1016/j.ophtha.2020.12.010>.
- [55] Wagshul ME, Lucas M, Ye K, Izzetoglu M, Holtzer R. Multi-modal neuroimaging of dual-task walking: Structural MRI and fNIRS analysis reveals prefrontal grey matter volume moderation of brain activation in older adults. *NeuroImage* 2019;189:745–54. doi: <https://doi.org/10.1016/j.neuroimage.2019.01.045>.
- [56] Wiener JM, Berthoz A, Wolbers T. Dissociable cognitive mechanisms underlying human path integration. *Exp Brain Res* 2011;208(1):61–71. doi: <https://doi.org/10.1007/s00221-010-2460-7>.
- [57] Wunderlich A, Gramann K. Landmark-based navigation instructions improve incidental spatial knowledge acquisition in real-world environments. *J Environ Psychol* 2021;77:101677. doi: <https://doi.org/10.1016/j.jenvp.2021.101677>.
- [58] Yogeve-Seligmann G, Hausdorff JM, Giladi N. The role of executive function and attention in gait. *Mov Disord* 2008;23(3):329–42. doi: <https://doi.org/10.1002/mds.21720>.
- [59] Zhong JY, Moffat SD. Extrahippocampal Contributions to Age-Related Changes in Spatial Navigation Ability. *Front Hum Neurosci* 2018;12:272. doi: <https://doi.org/10.3389/fnhum.2018.00272>.