Age-related differences in electrophysiological correlates of visuospatial reorientation

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Abstract

Spatial navigation abilities decline with age. Recent studies revealed a specific impairment in landmark-based reorientation, linked to changes in scene-selective brain regions activity. While fMRI studies suggest that these cortical modulations might be compensatory, a more precise investigation of the brain dynamics associated with visuospatial processing is warranted. We analyzed Event-Related Potentials and Event-Related Spectral Perturbations recorded from electrodes over scene-selective regions. 28 young adults and 28 older adults completed a desktop-based reorientation task using landmarks. Our findings show poorer reorientation performance among older adults. Signatures of age-related modulation of EEG activity imputable to scene-selective regions were predominantly observed within the right hemisphere. EEG analysis disclosed a tripartite worsening of scene processing accounting for older adults' difficulties. Firstly, a delayed and reduced P1 component likely reflects a slower and less efficient stimulus discrimination. Secondly, an increased N1 amplitude and theta-band activity suggest a higher demand on cognitive resources associated with more effortful processing of visuospatial information. Thirdly, a decreased P2 amplitude may imply deficient attentional mechanisms to select task-relevant stimuli.

Keywords:

Aging; ERP; ERSP; Spatial navigation; Visuospatial task; Landmarks

1. Introduction

Spatial navigation encompasses a complex set of behaviors that allow us to find our way and move in our environment. Although we are able to perform it effortlessly on a daily basis, successful navigation requires intricate cognitive processes such as sensory cue integration, working memory, or path integration (Wolbers & Hegarty, 2010), which are supported by a large and highly interconnected cerebral network (Ekstrom et al., 2017; Julian et al., 2018). Healthy aging is causally involved in the decline of spatial navigation abilities (Lester et al., 2017), with older adults experiencing difficulty in navigating both familiar and unfamiliar environments (Barrash, 1994). These impairments reduce the autonomy and mobility of older adults (Burns, 1999) resulting in an increased risk of progression of age-related disorders such as Alzheimer's disease (Coughlan et al., 2018). Given the general aging of the population, it is essential to gain a better understanding of the factors contributing to these age-related navigational deficits and their neural correlates.

Among all the information required for spatial navigation, the ability to perceive and integrate visuospatial information plays a crucial role for humans who depend predominantly on their visual system to interact with their surroundings (Ekstrom, 2015; Foo et al., 2005). Vision allows humans to recognize the environmental context in which they are navigating and to rapidly encode the navigability of a visual scene presented (Greene & Oliva, 2009). The extraction of visual landmarks that provide information-rich cues for their orientation is also sustained by this sensory modality, allowing an efficient human spatial navigation (Fischer et al., 2020). Authors have observed that greater visual attention is indeed devoted to these landmarks, which subsequently serve as crucial reference points for successful navigational behavior (de Condappa & Wiener, 2014; Hamid et al., 2010; Wenczel et al., 2017). However, the ability to use landmark information for navigation declines with age, as evidenced by several studies (Harris & Wolbers, 2012; Hartmeyer et al., 2017; Wiener et al., 2012). More recently, Bécu et al. (2023) extended these findings by unveiling a specific decline in landmark-based navigation (*i.e.,* encoding objects) but a preserved performance during geometry-based navigation (*i.e.,* encoding spatial layouts). These two navigation modalities exhibit specific neural signatures in young adults (Ramanoël et al., 2022) highlighting the importance of considering their neural correlates to gain insight into the specific deficits of older adults in landmark navigation.

The integration of spatial visual cues is mediated by a network of high-level visual brain regions. This network comprises three scene-selective regions: the Parahippocampal Place Area (PPA) (Epstein & Kanwisher, 1998), the Retrosplenial Complex (RSC, also referred as Medial Place Area, MPA) (Maguire, 2001; Silson et al., 2016), and the Occipital Place Area (OPA) (Dilks et al., 2013). The PPA, located in the parahippocampal cortex, is thought to be involved in the representation of the spatial layout (Kravitz et al., 2011) and in landmark recognition (Janzen & van Turennout, 2004; Sun et al., 2021), thus contributing to scene categorization (Persichetti & Dilks, 2018). The RSC, a region of the posterior cingulate cortex, is involved in the computation of heading directions (Gramann et al., 2021;

Marchette et al., 2014), the translation of information between egocentric and allocentric spatial reference frames (Vann et al., 2009; Zhang et al., 2012), and it may also combine visual and motor inputs for landmark encoding (Fischer et al., 2020). Finally, the OPA, which is located near the transverse occipital sulcus, supports first-person vision-guided navigation through its role in encoding environmental boundaries, local elements, and potential paths in a scene, which are also called navigational affordances (Bonner & Epstein, 2017; Epstein et al., 2017; Julian et al., 2018).

In the context of aging, several functional magnetic resonance imaging (fMRI) studies have highlighted age-related modifications in scene-selective regions during visual and spatial processing. Notably, reduced activity in the PPA has been observed to underpin age-related differences in the categorization of the fine-grained content of visual scenes (Ramanoël et al., 2015). Furthermore, the neural specificity and distinctiveness of the PPA and RSC have been shown to decline with age and to predict individual source and spatial memory abilities (Koch et al., 2020; Srokova et al., 2020). Regarding the OPA, fMRI acquisitions during a Y-maze reorientation task using objects as landmarks showed an increased activity of this region in older adults (Ramanoël et al., 2020). Critically, this age-related increase in parietal activity was only reported during the reorientation phase of the task involving landmark processing but not during free navigation (not involving reorientation). This finding was complemented by another brain connectivity study reporting a preserved structural connectivity around the OPA region and an increased functional connectivity between the OPA and PPA in older adults (Ramanoël et al., 2019).

Despite these results, how the temporal dynamics of scene-selective regions could contribute to the age-related navigational decline remains poorly characterized, mainly due to the limitations of fMRI in capturing brain processes at the millisecond timescale (Glover, 2011). With its high temporal resolution, Event-Related Potential (ERP) analysis represents a valuable neuroimaging approach for investigating early perceptual processes with electroencephalography (EEG). Notably, one ERP component, the occipito-parietal P2, has been proposed to be a marker of scene processing (Harel et al., 2016) and to reflect the activity of scene-selective regions (Kaiser et al., 2020). These results were complemented with intracranial EEG recordings suggesting that the activity of the OPA occurs in the time period of the P2 component (Vlcek et al., 2020). Recently, the amplitude of the P2 component was reported to scale linearly with the number of navigational affordances (Harel et al., 2022) reinforcing the P2 as a marker of scene-selective activity and more specifically of the OPA. Based on recordings from these occipito-parietal electrodes, Lithfous et al. (2014) reported an age-related increase of the P2 component amplitude and delayed P2 latency associated with an impaired performance on a spatial localization task. They suggested that changes of the parietal P2 component may reflect the mechanisms underlying the age-related decline in spatial processing and they emphasized the need for further studies to investigate P2 in relation to spatial memory or spatial visual cue processing. In a subsequent study using an EEG time-frequency analysis, Lithfous et al. (2018) found an increase in parahippocampal *theta* activity in high-performing older adults compared to young adults during a spatial navigation task. They

also found a decreased *theta* power in the group of low-performing older adult (*i.e.,* the group with the lowest accuracy in reproducing paths), reinforcing the proposed relationship between parahippocampal *theta* oscillations and successful navigation (Bohbot et al., 2017; Chrastil et al., 2022; Jacobs, 2014). These results highlight the potential of using EEG (Event Related Potential and time frequency analyses) to investigate the neural dynamics associated with reorientation impairment in older adults. However, none of these studies considered age-related differences in visuospatial processing despite the considerable impact of age on this cognitive function (Bécu et al., 2023; Segen et al., 2021). Indeed, aging is associated with declines in visual acuity (Faubert, 2002) and a reduced capacity for fine processing which may partially account for navigational impairments in older adults, even more so in environments where visual landmarks are the sole cues for reorientation (Ramanoël et al., 2015, 2020).

To address this caveat, the present study aims to examine age-related differences during a landmark-based reorientation task and the associated brain dynamics using EEG recordings from electrodes related to scene-selective brain regions (Harel et al., 2016; Kaiser et al., 2020). In order to investigate the contribution of age-related visuospatial processing declines in reorientation, we manipulated the level of perceptual difficulty, leading to the presentation of large and small landmarks. We hypothesized that older participants would exhibit a poorer navigational performance than young participants, especially when perceptual difficulty is increased (*i.e.,* when landmarks are smaller). At the cortical level, we expected that older adults would show higher parietal P2 amplitude and *theta* activity during reorientation than young adults, reflecting an increased involvement of the scene-selective regions.

2. Methods

2.1 Participants

We conducted the experiment on a sample population of 30 young participants and 32 healthy older participants. We removed 2 older participants from the analysis because they performed below chance level, and then we cannot ensure their comprehension of the task. In addition, 4 other participants (2 older and 2 young participants) were excluded due to excessive artefacts in the EEG data as assessed by signal-to-noise ratio calculation and a careful visual inspection of the signals. Analyses were finally conducted on 28 young participants (mean age: 23.93 years old; SEM = 0.64; range: 19-35; 14 females) and 28 older adults (mean age: 71.25 years old; SEM = 1.01; range: 61–81; 18 females). Participants were right-handed, had no history of neurological or psychiatric disorders and they self-reported normal or corrected-to-normal vision. They were assessed for cognitive impairment using the GRECO French version of the MMSE (Kalafat et al., 2003) with the proposed 26 cut-off to ensure their healthy cognitive status. They also completed a computerized version of the Spatial Orientation Task (Friedman et al., 2020). These results are presented and discussed in the Supplementary Materials (**Table S1**). The experiment was approved by the local Ethical Committee (CERNI-UCA no. 2021-050) and participants provided informed consent before starting the experiment.

2.2 Stimuli and procedure

Visual stimuli were created using the Unity Engine software (Unity Technologies version 2019.2.0.0f1) and presented on an iiyama ProLiteB2791HSU monitor (1920x1080, 30-83khz) placed at eye level and 60 cm away from the participants. Stimuli were presented using the open-source PsychoPy software (v2022.13), implemented on a Dell Precision 7560 computer (Intel® Xeon® W-11955).

The environment was adapted from a previous fMRI experiment on healthy aging (Ramanoël et al., 2020). It was a three-arm maze (Y-maze) consisting of three corridors: one branch containing a goal materialized by a gift box, 2 identical starting branches, and 3 three-dimensional (3D) objects positioned at the intersection serving as landmarks (a cube, a ball, and a pyramid). The experimental paradigm was divided into 3 tasks: learning, reorientation, and control (**Figure 1**). During the learning task, participants were passively moved through the maze at 2.5 virtual meter per second, with a rotation speed of 40 rad/s. They were instructed to memorize the path to the goal using the objects positioned at the intersection. Then, during the reorientation task, participants were presented with images of the intersection taken from the videos, and they were instructed to indicate the direction of the goal, as quickly and accurately as possible using their right hand to press the directional keys (left or right). These snapshots were extracted from either a near (at 4.25 virtual meters from the intersection) or a far perspective (at 11.2 virtual meters from the intersection) to modulate perceptual difficulty (hereafter referred to as *large* and *small* conditions, respectively). The average retinal visual angle of the landmarks in the small condition was 1.2°, while it was 2.5° in the large condition. Images were presented in a pseudo-randomized order (*i.e.,* a similar stimulus was presented no more than three times in a row) for 3 seconds each and were followed by auditory feedback depending on the correctness of the answer given. Afterwards, participants performed the control task which consisted of passively viewing images of the intersection, but this time with all 3 objects being identical (3 spheres, 3 cubes or 3 pyramids). They were instructed to look carefully at both the objects and the fixation cross presented between the different images. To mitigate the possibility of participants losing interest, we varied some properties of the environment (*i.e.,* wall texture and goal location), leading to the presentation of 15 different combinations, presented pseudo-randomly across participants. This sequence of learning, reorientation and control tasks was repeated 3 times for a total of 60 videos, 300 reorientation trials and 180 control trials, and a total acquisition time of 49 minutes.

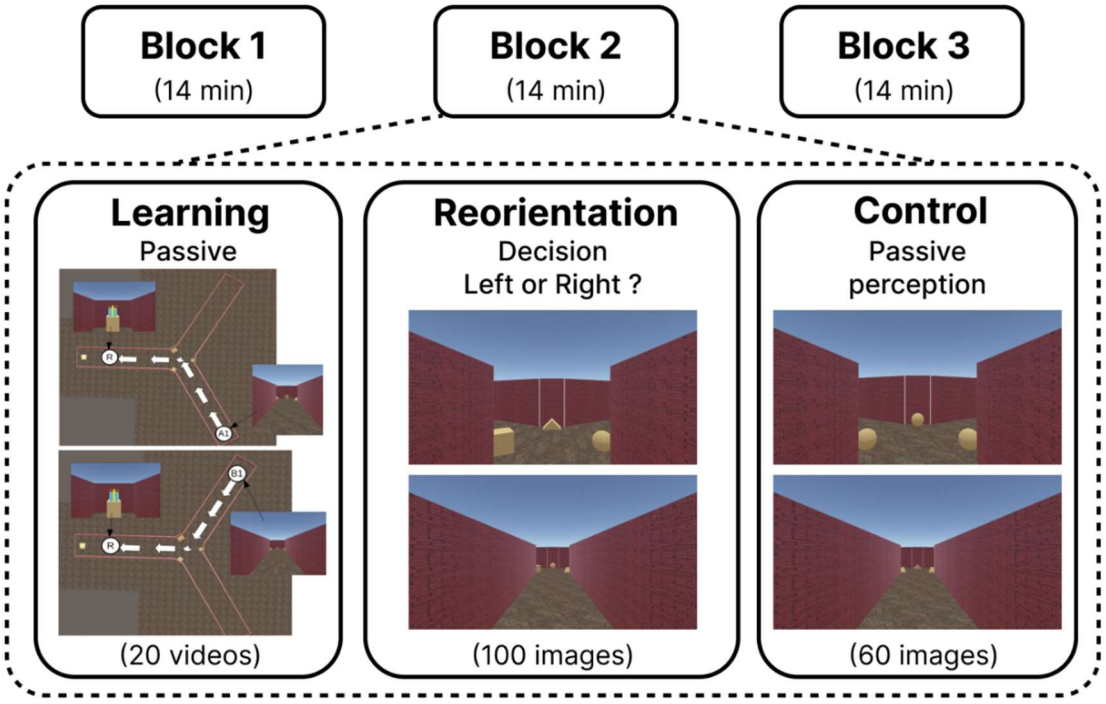

Figure 1. Presentation of the paradigm and some of the stimuli used. Blocks were the same between participants but were presented in a randomized order, with different wall textures. A short break was proposed to all participants between blocks

2.3 Recording and Analysis

2.3.1 EEG recording and preprocessing

EEG was sampled at 500 Hz from 64 Ag/AgCl electrodes mounted in a cap (Waveguard™ original) connected to an amplifier (eego™ mylab, ANT Neuro) and digitized at 24-bit resolution. Data were referenced to CPz electrode, with AFz as ground. Electrode impedances were reduced to at least 20 kΩ, with most values falling below 10 kΩ. Synchronization of EEG recording, and stimulus presentation was ensured by the LabStremingLayer software Labrecorder (LSL Labrecorder version 1.13). Offline preprocessing was performed with MATLAB (R2021a; The MathWorks Inc., Natick, MA, USA) using custom scripts based on the EEGLAB toolbox version 14.1.0b (Delorme & Makeig, 2004) and adapted from a previously used processing pipeline (Delaux et al., 2021).

We first downsampled the data to 250 Hz and corrected the time points for the software delay using the trigger time added to a fixed delay of 50ms for the hardware delay. We automatically removed line noise using the recently developed Zapline-Plus algorithm (Klug & Kloosterman, 2022). We then automatically identified and rejected noisy channels, using the default parameters proposed in the PREP pipeline (Bigdely-Shamlo et al., 2015). On average, 4.25 channels were rejected (SEM= 0.39). These channels were then reconstructed by spherical interpolation of neighboring channels, and the data were re-referenced to the common average. Artifacts were automatically rejected using Artifact Subspace Reconstruction (ASR) (Kothe & Jung, 2015) which uses clean portions of the data to determine thresholds for rejecting components. We used an ASR cutoff parameter of 20, corresponding to the

proposed optimal range between 10 and 100 (Chang et al., 2020). We then temporally high-passed the cleaned dataset using a 1.5 Hz Finite Impulse Response (FIR) filter with a Hamming window (with 0.5 Hz transition bandwidth, 1.25 Hz passband edge, and 1650 order) (Klug & Gramann, 2021) before applying independent component analysis (ICA) using the Adaptative Mixture Independent Component Analysis (AMICA) algorithm (Palmer et al., 2008). Next, each independent component (IC) was assigned a dipolar source reconstructed with the equivalent dipole model (DipFit ; Oostenveld & Oostendorp, 2002). We used the ICLabel algorithm (Pion-Tonachini et al., 2019) to classify components into 7 classes, using default percentages for classification. We opted for a conservative approach and on average, we retained 14.64 components (SEM = 0.67) corresponding to brain activity. Next, we applied a bandpass filter to the data, with a lower cutoff frequency of 0.3 Hz (with 0.5 Hz transition bandwidth, 0.55 Hz passband edge, and 1650 order) to remove slow drifts, and an upper cutoff frequency of 80 Hz (20 Hz transition bandwidth, 80 Hz passband edge, and 42 order) to attenuate high-frequency noise and muscle artifacts. Finally, the preprocessed data were segmented into epochs ranging from -200 ms before to 600 ms after stimulus onset for all conditions. Epochs were excluded from the analysis if less than 90% of the period was clean. On average, we kept 76.56% of the epochs (mean epochs kept per subject: 367.50; SEM = 2.60). The number of epochs extracted was the same for both age groups ($t_{(1,43.33)}$ = 0.820, p = 0.417).

2.3.2 Event Related Potential and time-frequency analyses

Analyses were restricted to the occipito-parietal electrodes previously associated with scene-selective regions (Harel et al., 2016; Kaiser et al., 2020), corresponding to P6-P8-PO8 for the right hemisphere and P5-P7-PO7 for the left hemisphere. Further data analysis was performed using custom MATLAB scripts with functions from the Fieldtrip toolbox (Oostenveld et al., 2011).

For the Event Related Potentials (ERPs), the baseline was identified from -200 ms to image onset corresponding to the recommended minimum of 10 to 20% total epoch length (Luck, 2014), and mean baseline activity was subtracted from the data. Peak amplitude was calculated using the mean amplitude, corresponding to the average of the most positive value surrounded by two lower values. Given the reported effect of aging on peak latency (Kropotov et al., 2016; Mueller et al., 2008), we decided to calculate P1, N1, and P2 latency for each age group. Then, we took a 100 ms wide window around this value to extract the latencies and amplitudes of the individual components.

Time-frequency analysis was performed using the superlet approach (Moca et al., 2021), a spectral estimator that uses sets of increasingly constrained bandwidth wavelets to achieve time-frequency super-resolution. For this purpose, we used the Fieldtrip function ft_freqanalysis to decompose between 1 and 80 Hz, using a width of 2 and a Gaussian width of 3, with an increasing order scaling from 1 to 80. Once the decomposition was completed, we computed event-related spectral perturbations (ERSPs) (Makeig, 1993). We used the decibel conversion to normalize power values with a baseline between -250 and -50 ms due to temporal smearing (see Cohen, 2014 for more details).

2.3.3 Statistical analysis

For the ERSPs, we performed a non-parametric cluster-based permutation test using a Monte-Carlo estimate to deal with the multiple comparisons problem (Maris & Oostenveld, 2007). We chose the most robust and least conservative method among several modalities, which involved 10 000 permutations with weighted cluster mass (Hayasaka & Nichols, 2004) and a cluster-level *alpha* of 0.005 to account for multiple comparisons. All other statistical analyses were performed using R Statistical Software (version 4.2.1, R Foundation for Statistical Computing, Vienna, Austria) with R studio (version 2022.07.02+576). After comparing different models using the Akaike information criterion (Akaike, 1974), we decided to use the linear mixed model from the lme4 R package (Bates et al., 2014), with participants included as random intercept. Then, we used the anova function to compute a type III Analysis of Variance (ANOVA) using Satterthwaite's method. The reported results are estimated marginal means computed with the emmeans package in R, using a type III sum of squares, and finally post-hoc Tukey's Honest Significant Difference tests were performed. To ensure normality of residuals and homoscedasticity, both were carefully visually inspected using quantile-quantile plots and boxplots, respectively. Finally, we conducted correlation analyses between ERP peaks and behavioral data using the Bonferroni correction to account for multiple comparisons.

3. Results

3.1 Behavioral results

We observed age-related differences in navigation performance. In terms of accuracy **(Figure 2.A**), we reported only a main effect of age ($F_{(1,54)} = 6.63$, $p = 0.013$, $\eta_p^2 = 0.11$, 95% CI = [0.00, 0.28])), with lower accuracy for older adults (M = 93.4% , SE = 0.94) compared to young adults (M = 96.8% , SE = 0.94). There was neither an effect of condition ($F_{(1,54)} = 0.527$, $p > 0.47$) nor an interaction between the factors ($F_{(1,54)} = 0.136$, $p > 0.71$). Regarding the reaction time (**Figure 2.B**), we found a main effect of age ($F_{(1,54)} = 40.97$, $p < 0.001$, $\eta_p^2 = 0.43$, 95% CI = [0.24, 0.58]) in older adults (M = 1162 ms, SE = 35.2) who had a longer reaction time than young adults (M = 843 ms , SE = 35.2). We also found a main effect of condition ($F_{(1,54)} = 52.47$, $p < 0.001$, $\eta_p^2 = 0.48$, 95% CI = [0.30, 0.63]) with a higher reaction time for the small condition (M = 1020 ms, SE = 25) compared to the large condition (M = 985 ms, SE = 25) for both young and older adults. There was no interaction between age and condition ($F_{(1,54)} = 1.48$, $p = 0.229$).

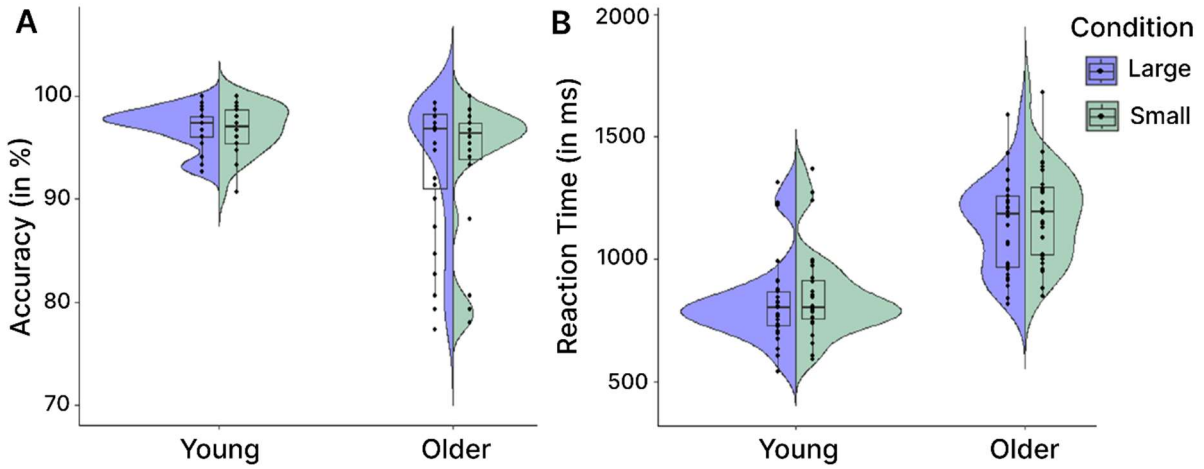

Figure 2. Performance of participants in the reorientation task. Individual points represent the average for each participant. **A**. Accuracy computed as the percentage of reorientation errors over all trials. **B.** Reaction time between the presentation of the stimulus and the recorded response.

3.2 ERPs results for large and small conditions during reorientation

In this analysis we compared the large and small conditions to examine the effect of age with perceptual difficulty during the reorientation task (**Figure 3**).

P1, N1, and P2 amplitudes

First, we evaluated the age effect by comparing the EEG recordings of young and older adults. We found no main effect of age for P1 amplitude ($F_{(1,54.17)} = 2.57$, $p = 0.11$), but a higher amplitude for young than older adults when considering only the right hemisphere ($t_{(67)} = 3.02$, $p = 0.018$, d = 1.29, 95% CI = [0.43, 2.15]). We reported an increased N1 amplitude (*i.e.,* more negative) for older adults compared to young adults ($F_{(1,54.09)} = 28.92$, $p < 0.001$, $\eta_p^2 = 0.35$, 95% CI = [0.16, 0.51]) in both hemispheres. We also observed a lower P2 amplitude in older adults compared to young adults ($F_{(1,54)} = 7.36$, $p < 0.001$, $\eta_p^2 = 0.12$, 95% CI = [0.01, 0.29]) but this age effect was restricted to the right hemisphere ($t_{(68)} = 4.58$, $p < 0.001$, d = 1.82, 95% CI = [-1.00, 2.62]), with no difference for the left hemisphere ($t_{(68.3)} = 0.53$, $p = 0.95$).

Next, we considered the effect of condition comparing large *vs.* small. We found a higher P1 amplitude for the small condition compared to the large condition ($F_{(1,159.25)} = 4.91$, $p = 0.028$, $\eta_p^2 = 0.03$, 95% CI = [0.00, 0.10]). There was no modulation of either N1 ($F_{(1,159)} = 3.43$, $p = 0.066$), or P2 amplitudes ($F_{(1,162)} = 1.70$, $p = 0.19$).

Finally, we examined the lateralization effect by directly comparing the brain signals from the right and left hemispheres. We reported a higher amplitude for P1 in the right hemisphere ($F_{(1,159.77)} = 33.74$, $p < 0.001$, $\eta_p^2 = 0.17$, 95% CI = [0.08, 0.28]), but this effect was restricted to young adults, as older adults showed no lateralization ($t_{(159)} = 0.76$, $p = 0.87$). For P2, we found a higher amplitude in the right hemisphere independent of age group ($F_{(1,162)} = 122.29$, $p < 0.001$, $\eta_p^2 = 0.43$, 95% CI = [0.32, 0.52]). Considering N1, we observed the opposite, with a greater amplitude in the left hemisphere ($F_{(1,159.79)} =$

15.15, $p < 0.001$, $\eta_p^2 = 0.09$, 95% CI = [0.02, 0.18]). This effect was restricted to young adults ($t_{(160)} = 5.13$, $p < 0.001$, d = 0.99, 95% CI = [0.60, 1.39]), whereas older adults presented similar N1 activity for both hemispheres ($t_{(159)} = 0.32$, $p = 0.99$).

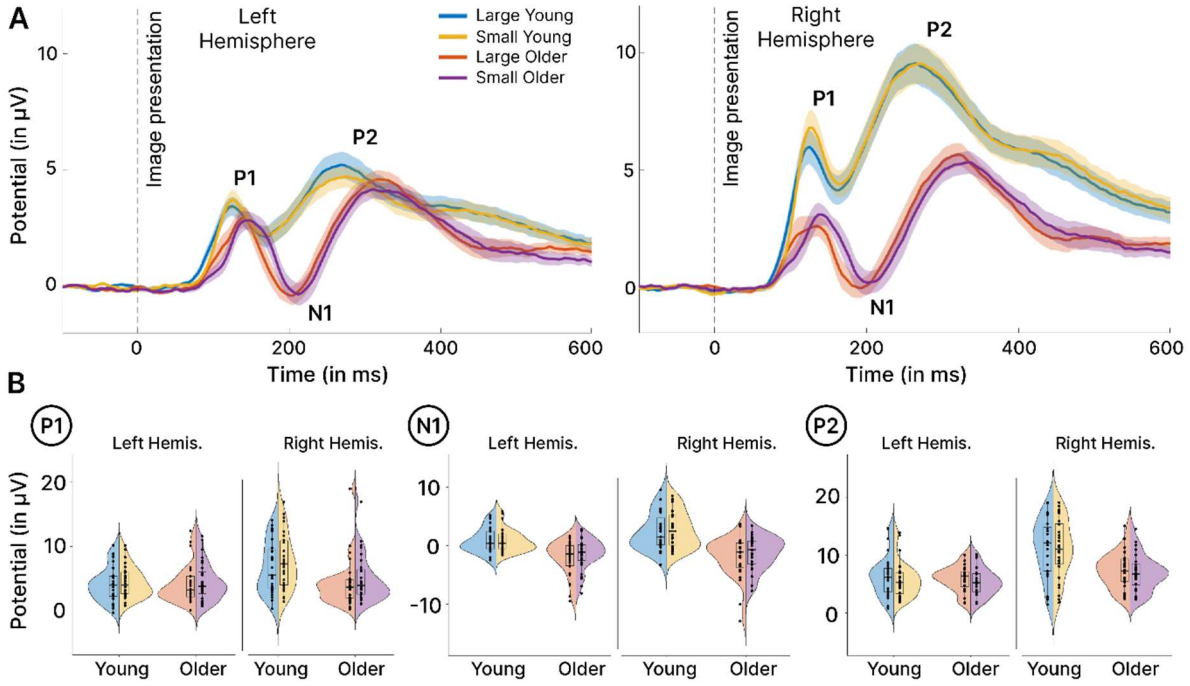

Figure 3. ERP results for near and far conditions during the reorientation task. **A.** Grand-average ERPs considering age (young/older), condition (large/small) and hemisphere (left/right) as variables, individually baselined corrected. Activity averaged over P6-P8-PO8 electrodes for the right hemisphere and over P5-P7-PO7 electrodes for the left hemisphere. **B.** Split violin plot of extracted individual amplitudes for P1, N1 and P2 component. Statistics were computed using these values.

P1, N1, and P2 latencies

Looking at the age effect, we found later peaks for older adults in P1 ($F_{(1,54.35)} = 13.12$, $p < 0.001$, $\eta_p^2 = 0.19$, 95 % CI = [0.04, 0.37]), N1 ($F_{(1,53.92)} = 37.24$, $p < 0.001$, $\eta_p^2 = 0.41$, 95 % CI = [0.21, 0.56]) and P2 ($F_{(1,54)} = 130.25$, $p < 0.001$, $\eta_p^2 = 0.71$, 95% CI = [0.57, 0.79]). The effect for P1 was restricted to the small condition ($t_{(77)} = 4.76$, $p < 0.001$, d = 1.57, 95% CI = [0.90, 2.24]) as we reported no age difference for the large condition ($t_{(77)} = 1.85$, $p = 0.26$).

Considering the condition effect, we observed a delayed P1 for the small condition compared to the large condition ($F_{(1,159.53)} = 20.89$, $p < 0.001$, $\eta_p^2 = 0.12$, 95% CI = [0.04, 0.21]). This effect was not present for either N1 ($F_{(1,159.28)} = 1.85$, $p = 0.544$), or P2 ($F_{(1,162)} = 1.52$, $p = 0.22$). This condition effect for P1 was present only for older adults ($t_{(159)} = 5.80$, $p < 0.001$, d = 1.10, 95% CI = [0.71, 1.49]) with no difference for young adults ($t_{(159)} = 0.70$, $p = 0.90$).

Finally, concerning lateralization, we found no effect for P1 ($F_{(1,160.32)} = 3.76$, $p = 0.054$) or N1 ($F_{(1,160.41)} = 3.64$, $p = 0.058$). For P2, we observed a later peak in the right hemisphere compared to the left hemisphere ($F_{(1,162)} = 4.14$, $p = 0.043$, $\eta_p^2 = 0.03$, 95% CI = [0.00, 0.54]).

3.3 ERP results comparing reorientation and control tasks

In this second analysis, we compared the activity elicited by the reorientation task and the control task, in order to dissociate reorientation from pure scene perception effects. The results presented below correspond to the large and small conditions merged together (**Figure 4**). Before doing so, we checked that the same pattern of results was obtained when the two conditions were considered separately.

P1, N1 and P2 Amplitudes

First, we examined the age effect, comparing young and older adults. We found no effect for P1 amplitude ($F_{(1,54.06)} = 2.15$, $p = 0.15$), but a higher amplitude for young adults when considering the right hemisphere only ($t_{(68)} = 2.99$, $p = 0.019$, d = 1.21, 95% CI = [0.39, 2.02]), with no age difference in the left hemisphere ($t_{(67.6)} = 0.23$, $p = 0.996$). We found a higher N1 amplitude (*i.e.,* more negative) for older adults ($F_{(1,54.08)} = 31.82$, $p < 0.001$, $\eta_p^2 = 0.37$, 95% CI = [0.18, 0.53]), and the opposite pattern for P2, with a higher amplitude for young adults ($F_{(1,84)} = 10.33$, $p = 0.002$, $\eta_p^2 = 0.16$, 95% CI = [0.02, 0.34]).

We then considered the task and compared reorientation and control (*i.e.,* passive perception). We found a similar pattern, with a higher amplitude for the reorientation task for P1 ($F_{(1,161.14)} = 4.32$, $p = 0.040$, $\eta_p^2 = 0.03$, 95% CI = [0.00, 0.09]), N1 ($F_{(1,161.16)} = 13.90$, $p < 0.001$, $\eta_p^2 = 0.08$, 95% CI = [0.02, 0.17]) and P2 ($F_{(1,162)} = 44.38$, $p < 0.001$, $\eta_p^2 = 0.22$, 95% CI = [0.11, 0.32]). Considering only N1 amplitude, the effect was limited to older adults ($t_{(159)} = 3.98$, $p < 0.001$, d = 0.75, 95% CI = [0.37, 1.14]), as young adults showed no difference between reorientation and control for this component ($t_{(161)} = 1.30$, $p = 0.57$).

Finally, we considered laterization, comparing the left and right hemispheres. We reported a similar pattern for positive components, with a higher amplitude in the right hemisphere for P1 ($F_{(1,161.14)} = 32.22$, $p < 0.001$, $\eta_p^2 = 0.17$, 95% CI = [0.07, 0.27]) and P2 ($F_{(1,162)} = 95.95$, $p < 0.001$, $\eta_p^2 = 0.37$, 95% CI = [0.26, 0.47]). These results were only observed for young adults, as older adults showed no lateralization effect for either the P1 ($t_{(161)} = 0.58$, $p = 0.94$) or the P2 component ($t_{(162)} = 2.43$, $p = 0.12$). For N1, we found the opposite result, with a higher amplitude for the left hemisphere ($F_{(1,161.16)} = 14.83$, $p < 0.001$, $\eta_p^2 = 0.08$, 95% CI = [0.02, 0.18]), again only for young adults ($t_{(159)} = 5.94$, $p < 0.001$, d = 1.13, 95% CI = [0.73, 1.52]) with no lateralization for older adults ($t_{(161)} = 0.51$, $p = 0.96$).

P1, N1 and P2 Latencies

First, we observed a similar pattern for age differences across components, with a later peak for P1 ($F_{(1,54.06)} = 12.12$, $p < 0.001$, $\eta_p^2 = 0.18$, 95% CI = [0.04, 0.36]), N1 ($F_{(1,53.87)} = 47.88$, $p < 0.001$, $\eta_p^2 = 0.47$, 95% CI = [0.28, 0.61]) and P2 ($F_{(1,54)} = 154.14$, $p < 0.001$, $\eta_p^2 = 0.74$, 95% CI = [0.62, 0.82]). The age difference for P1 was present in the left hemisphere only ($t_{(69.8)} = 4.16$, $p < 0.001$, d = 1.58, 95% CI

= [0.81, 2.35]), as we reported no age-related modulation of P1 for the right hemisphere ($t_{(70)} = 2.36$, $p = 0.10$).

When comparing reorientation and control tasks, there was no difference in P1 latency ($F_{(1,161.15)} = 0.08$, $p = 0.77$). We observed a similar pattern for the other two components, with a later peak for the reorientation task for N1 ($F_{(1,161.01)} = 9.34$, $p = 0.003$, $\eta_p^2 = 0.05$, 95% CI = [0.01, 0.14]) and P2 ($F_{(1,162)} = 58.59$, $p < 0.001$, $\eta_p^2 = 0.27$, 95% CI = [0.16, 0.37]).

For lateralization, comparing left and right hemispheres, we observed a later P1 peak for the left hemisphere ($F_{(1,161.15)} = 4.96$, $p = 0.027$, $\eta_p^2 = 0.03$, 95% CI = [0.00, 0.10]), with a similar pattern for the N1 component ($F_{(1,161.01)} = 6.31$, $p = 0.013$, $\eta_p^2 = 0.04$, 95% CI = [0.00, 0.11]). Considering P2, we found no difference between the left and right hemispheres ($F_{(1,162)} = 1.17$, $p = 0.28$). The later P1 peak was observed for older adults only ($t_{(161.2)} = 3.39$, $p = 0.005$, d = 0.64, 95% CI = [0.26, 1.02]).

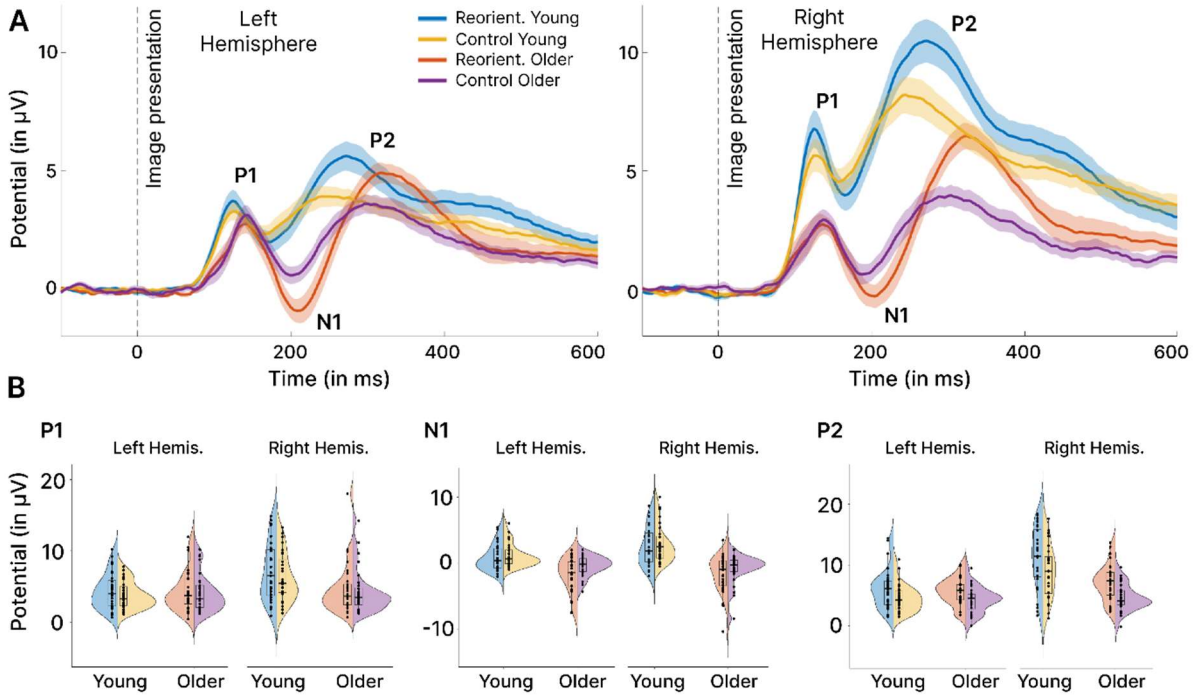

Figure 4. ERP results comparing reorientation and control tasks. **A.** Grand-average ERPs considering age (young/older), task (reorientation/control) and hemisphere (left/right) as variables, individually baselined corrected. Activity averaged over P6-P8-PO8 electrodes for the right hemisphere and over P5-P7-PO7 electrodes for the left hemisphere. **B.** Split violin plot of extracted individual amplitudes for P1, N1 and P2 components. Statistics were computed using these values.

3.4 ERSP results comparing reorientation and control tasks

Finally, we examined brain oscillations by computing ERSP. This allowed us to examine additional information about the underlying cognitive process beyond ERPs (Herrmann et al., 2014).

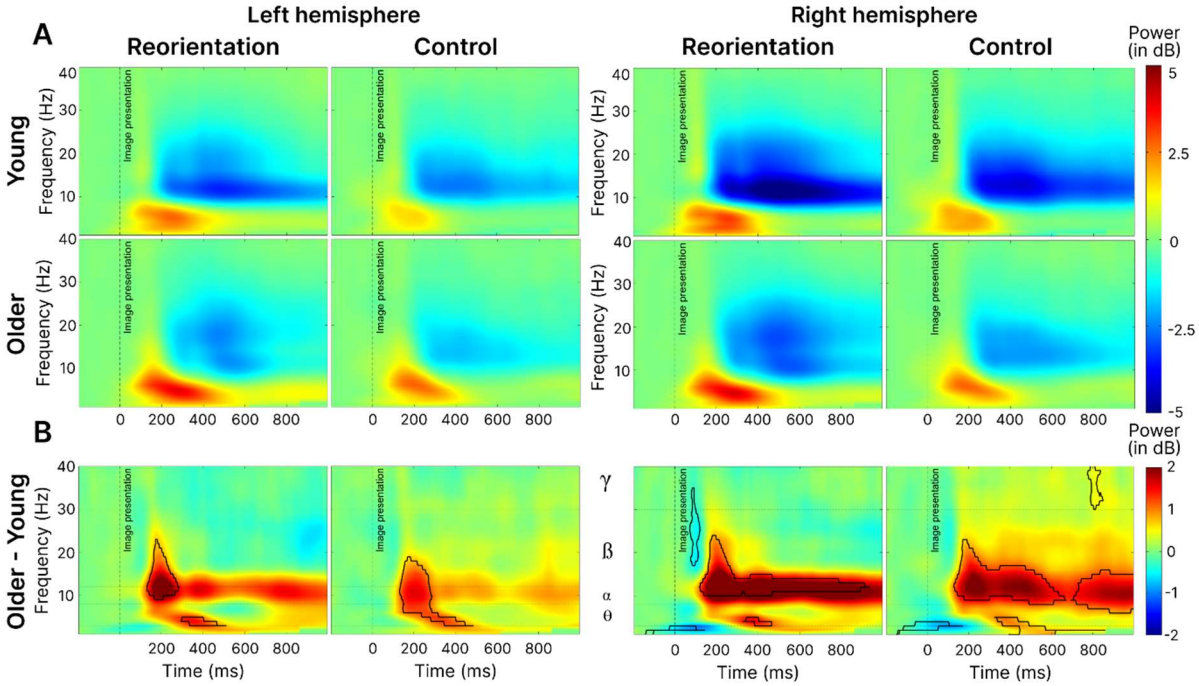

Figure 5. ERSP results comparing reorientation and control tasks. **A.** Grand-average ERSPs, considering age (young/older), task (reorientation/control) and hemisphere (left/right) as variables, using decibel baseline (-150 to -50 ms) normalization. Activity averaged over P6-P8-PO8 electrodes for the right hemisphere and over P5-P7-PO7 electrodes for the left hemisphere. **B.** ERSP activity of older minus young adults. The black line corresponds to cluster-based permutation tests results with p-value < 0.05.

For all ERSP analyses (**Figure 5.A**.), we found a similar pattern consisting of an increased synchronization (*i.e.,* an increase in power interpreted as an increase in neural firing synchronization of the underlying neuronal population compared to the selected baseline) in low frequency bands, *delta*/*theta* (1-8 Hz), occurring 50 ms before image presentation for young adults and lasting up to +400 ms and up to +500 ms for older adults in the reorientation task. This synchronization was followed by desynchronization in the higher frequency bands *alpha* (8-13 Hz) and *beta* (13-30 Hz). We then conducted a cluster-based permutation tests on these results (**Figure 5.B.**). In the right hemisphere, we reported a decreased synchronization in the *alpha/beta* band in older adults compared to young adults, starting from +200 ms and lasting until +1000 ms. In the left hemisphere, this result was significant only within a short window around +200 ms. We also reported a decreased synchronization in the *delta* (1-3 Hz) band for older adults compared to their younger counterparts, starting from 50 ms before image presentation up to +200 ms. Older adults also showed an increase in *theta* (3-8 Hz) synchronization, with a burst starting just after +200 ms and lasting up to +400 ms, and a decrease in high *beta* band synchronization for the reorientation task specific to the right hemisphere.

3.5 Correlation analyses between ERP and Behavioral data

We performed correlational analyses between ERP (peak amplitudes and latencies) and behavioral data (reaction times and accuracies), separately for young and older adults. This resulted in a total of 48

comparisons, with no significant results after Bonferroni correction. A table with all the uncorrected *p*-values is available in the Supplementary Materials (Table S2).

4. Discussion

This EEG study aimed to investigate age-related differences during a landmark-based reorientation task and their neural correlates. Consistent with previous studies, our results indicate that older adults demonstrate reduced navigational abilities, as evidenced by slower and less precise reorientation. However, in contrast with our initial hypothesis, the perception of landmarks of different sizes was not a deteriorating factor for older adults' performance on the task, even though it was associated with a delayed P1 component in older adults only. Age-related reorientation deficits were associated with differences in the neural dynamics of high-level visual processing. Indeed, we found delayed latencies of the P1, N1 and P2 components recorded from occipito-parietal electrodes associated with scene-selective regions. Moreover, older adults displayed decreased P1 and P2 amplitudes as well as lower *alpha*/*beta* desynchronization in the right hemisphere specifically. Finally, only older adults exhibited increased N1 amplitude in both hemispheres for the reorientation task, accompanied by higher levels of *theta* power. These results points toward a three-part process that may contribute to older adults' difficulties in landmark reorientation, involving slower and less efficient visual processing, more effortful processing of visuospatial information, and a deficit in the attentional mechanism related to the selection of task-relevant stimuli.

Reorientation performance is impaired in aging and reaction time decreases similarly for both age groups when perceptual difficulty increases

The behavioral results indicated that young adults performed better, with a lower reaction time and a higher rate of recovered paths. These results support previous findings that older adults are impaired during a navigation task which solely relies on the use of visual landmarks for reorientation (Bécu et al., 2023; West et al., 2023). It is worth mentioning, that despite their diminished performance, older adults still achieved a high level of accuracy which may be explained by the relative simplicity of the task and their healthy cognitive status. Increasing perceptual difficulty (*i.e.,* decreasing landmark size) did not increase error rate, but it did lead to an increase in reaction time in both age groups. This finding is consistent with the well-characterized relationship between stimulus size and reaction time (Plewan & Rinkenauer, 2017; Sperandio et al., 2009). However, contrary to our hypotheses, older adults did not show greater difficulty than young adults when perceptual difficulty was manipulated. This lack of behavioral difference is in line with our EEG findings, which showed no interaction effect between perceptual difficulty and age; both age groups displayed a similar increase in P1 amplitude in the small landmark condition. However, we reported a later P1 peak amplitude only for older adults in the small condition compared to the large condition. It has been suggested that the P1 component is modulated by visuospatial attention (Di Russo et al., 2003), but the exact functional basis of this effect remains

391 debated. The "P1 inhibition-timing" model proposed by Klimesch et al. (2007, 2011) suggests that the
392 P1 reflects a transient inhibitory filter that operates to increase the signal-to-noise ratio allowing an
393 efficient early categorization process. This component may be the earliest index of attentional control,
394 being increased over posterior regions when processing complexity is high (Fellinger et al., 2012).
395 Moreover, the fact that older adults presented a decreased P1 amplitude suggests that they may have
396 impairments in the early categorization process of visual stimuli which are exacerbated by the
397 reorientation task. Then, when faced with increased perceptual difficulty older adults required more time
398 to allocate greater attentional resources to the harder perceptual task (Sawetsuttipan et al., 2023). These
399 findings align with the two leading cognitive aging hypotheses which posit that aging is associated with
400 an inhibitory deficit (*i.e.,* decreased P1 amplitude) and the processing speed hypothesis, (*i.e*., increased
401 P1 latency) when the perceptual difficulty of the task is increased (Finnigan et al., 2011; Gazzaley et al.,
402 2008). It is worth noting that although there was a difference in P1 latency, neither age-related
403 modulation was observed for the later components (namely, N1 and P2) nor for behavioral data. This
404 suggests that the delay in P1 latency may not significantly affect performance with a possible later
405 mechanism compensating for this early delay.

406 ***N1 amplitude and theta power reflects increased resources allocation for landmark processing by***
407 ***older adults***

408 Regarding the N1 component, we observed that older adults exhibited an increased amplitude in both
409 hemispheres compared to young adults. Additionally, we found that older adults had a higher N1
410 amplitude during the reorientation phase than during passive perception, and that this pattern was not
411 observed in young adults. Some authors have suggested that the N1 component reflect enhanced visual
412 information processing (Luck, 1995; Vogel & Luck, 2000) and visual stimuli discrimination (Finnigan
413 et al., 2011; Hillyard et al., 1998; Hopf et al., 2002; Warbrick et al., 2014; Wiegand et al., 2014). The
414 N1 was previously associated with the activity of the posterior precuneus (Natale et al., 2006). This
415 region plays a role in allocating attention to spatial information, encoding and retrieving spatial
416 memories, and identifying and using relevant landmarks (Cona & Scarpazza, 2019; Delaux et al., 2021).
417 Intracranial EEG recordings also pointed out the activity of the precuneus activity occurring around
418 210ms after the presentation of a stimulus, while also highlighting the activity of the PPA around 170ms
419 (Bastin et al., 2013; Vlcek et al., 2020). During the same time window as the N1 component, we also
420 observed an increase in *theta* activity. The link between *theta* power and the N1 component was
421 proposed by Klimesch et al. (2004) arguing that the power in the N1 time window was generated
422 primarily by frequencies in the *theta* range (Gruber et al., 2005; Van der Lubbe et al., 2016). Here, we
423 observed an increased *theta* synchronization during the reorientation task, which was more pronounced
424 in older adults, with a burst occurring after 200ms. This increase in *theta* activity was also observed by
425 Lithfous et al. (2018) during a maze reorientation task and associated with better performance in the
426 older group. They interpreted their results as a possible compensatory mechanism exhibited by high-

performing older adults, which highlights the importance of parietal *theta* activity for a successful visually-guided navigation (Chrastil et al., 2022). Taken together our results emphasize the role of the N1 component in landmark-based spatial navigation in the context of aging. They provide evidence for an increased bilateral activity in the *theta* band on electrodes associated with scene-selective regions suggesting that older adults resort to more extensive neural resources to process visual landmarks.

Age-related decrements in selective attention during task-relevant information processing

Regarding the P2 component, we found that older adults exhibited a reduced amplitude compared to younger adults. Conversely, we observed a similar enhancement of amplitude in both age groups when they performed the reorientation task versus the passive perception. These results seem to indicate that the age-related decrease in P2 amplitude reflects a general impairment in the capacity to complete a visual discrimination task, regardless of the reorientation task. The literature has proposed that this posterior P2 component may reflect the mediation of information between memory systems, as a way to compare visual inputs and information stored in the working memory (Cepeda-Freyre et al., 2020; Freunberger et al., 2007; Lefebvre et al., 2005). Other recent findings suggest that the P2 component may rather represent a top-down attentional control during visual processing of objects (Lai et al., 2020), indicating enhanced selective attention by task-relevant stimulus (Freunberger et al., 2007; Mecklinger et al., 2009; Philips & Takeda, 2009). As we observed a similar age-related decrease in a task that did not involve working memory (*i.e.*, a passive perception), we argue that the P2 amplitude decrease we report may reflect the well-supported age-related decline in top-down selection of task-relevant objects, which are the landmarks in our case (Lai et al., 2020). However, we cannot exclude that this decrease in P2 amplitude among older adults could also be ascribed to the decline in spatial working memory due to cognitive aging as reported in previous studies (Finnigan et al., 2011; Klencklen et al., 2012). This proposed age-related decrease in spatial information processing is also supported by our ERSP results, showing a decrease of *alpha/beta* desynchronization among older adults. It has been suggested that these frequency bands support the endogenous activation of neuronal ensembles involved in task-relevant information processing (Griffiths et al., 2019; Hanslmayr et al., 2012; Spitzer & Haegens, 2017). They were also previously observed during good reorientation choices in spatial navigation task (Chrastil et al., 2022), interpreted as the reflect of memory retrieval process (Klimesch, 1997, 1999). Finally, we hypothesized an increase in P2 amplitude with aging, in light of the findings from Ramanoël et al. (2020) who reported an increase in OPA activity among older adults during active reorientation, the OPA activity proposed to be reflected in the parietal P2 component (Harel et al., 2016, 2022; Kaiser et al., 2020). However, in their work, Ramanoël et al. (2020) had subjects actively navigate in the maze, and used fMRI recordings, which have some important differences that may account for the differences we observed. Moreover, the OPA may not be the only scene-selective brain regions contributing to the P2 component, and spatial sensitivity of scalp EEG does not allow us to distinguish between OPA and PPA for example. This was suggested by Kaiser et al. (2020) who also reported, along with OPA, activity of

463 the PPA during this time window which was proposed in an iEEG study to last for thousands of
464 milliseconds (Vlcek et al., 2020), possibly overlapping over occipito-parietal electrodes (Persichetti &
465 Dilks, 2019).

466 ***Aging decreases lateralization of visuospatial processing***

467 Finally, we found a distinct lateralization of brain activity in young adults, with greater activation
468 observed in the right hemisphere than in the left hemisphere during both the passive perception and
469 reorientation phases of the experiment. Harel et al. (2016, 2022) similarly observed higher amplitudes
470 in the right hemisphere among young adults only, during a passive scene perception task. This is
471 consistent with the commonly accepted notion that selective spatial attention and spatial working
472 memory are controlled by a predominantly right hemisphere network (Awh & Jonides, 2001; Young,
473 2012). This also appears to hold true during human spatial navigation as reported in a meta-analysis of
474 47 fMRI studies (Li et al., 2021). In our results, this lateralization was weaker among older adults for
475 P1 and P2 components, and amplitude was lower in the right hemisphere among older adults only. Using
476 a visuospatial task, Learmonth et al. (2017) also reported decreased right hemisphere control among
477 older adults during a visuospatial task and our results confirm the hypothesis of right hemisphere
478 engagement decrease with age as proposed by the right hemi-aging model (Dolcos et al., 2002). This
479 result also highlights the importance of considering both hemispheres separately when conducting ERP
480 or ERSP investigations of age-related modifications.

481 ***Limitations and perspectives***

482 One of the main limitations of our results is that we did not find any correlation between behavioral and
483 EEG data. This can be explained by the relative behavioral simplicity of our task, which may have
484 prevented us from capturing subtle variations in performance. Furthermore, concerning the modulations
485 of the P1, N1, and P2 components, their interpretation in an independent way could be exaggerated as
486 we acknowledge the possibility that effects observed on later peaks may depend on preceding peaks.
487 For instance, it is conceivable that P1 modulations may exert an effect on N1 peak, rendering the
488 conventional label "component" potentially misleading (Luck, 2005).

489 In an effort to disentangle reorientation from passive perception, we introduced a cognitive load
490 disparity between the two tasks, which may account in part for the observed results, particularly for the
491 P2 component. To address this issue, future investigations might consider including control tasks relying
492 on stimulus detection and decision-making paradigms, such as the N-back task. Finally, given the
493 changes in visual exploration between young and older adults and their impact on information
494 processing (Bécu et al., 2020, 2023; Durteste et al., 2023; Ryan et al., 2022) it would be worthwhile to
495 investigate the effect of age on gaze patterns during a landmark-based reorientation task, linking EEG
496 with eye-tracking data to gain more insight into how older adults are impaired in using landmarks during
497 reorientation.

5. Conclusion

Our study aimed to investigate age-related differences in visuospatial processing and the underlying brain dynamics within scene-selective regions in young and healthy older adults performing a landmark-based reorientation task. Older adults showed reduced reorientation performance along with increased latency of early cortical markers of visual processing in scene-selective regions, suggesting that navigational deficits may result from delayed processing of visuospatial information. Decreasing landmark size and thus increasing perceptual difficulty led to a delayed P1 component only in older adults, suggesting an age-related delayed early categorization of smaller landmarks. Our EEG data also revealed a three-part process that may partially account for older adults' challenges during landmark reorientation. First, a delayed and reduced P1 component indicated slower and less efficient visual processing, including stimulus discrimination. Second, the increase in N1 amplitude and theta-band activity indicated a greater demand on cognitive resources, leading to more effortful processing of visuospatial information. Third, the reduction in P2 amplitude associated with *alpha-beta* activity suggested a deficiency in the attentional mechanism for selecting task-relevant stimuli. Finally, our findings underscore the importance of considering both hemispheres separately when studying aging, as they highlight an age-related decrease in right hemisphere specific activity. Taken together, these results highlight the interest of using EEG to gain insight into age-related modulations of neural correlates of visuospatial processing during reorientation, while paving the way for further investigations to better characterize the brain dynamics underlying spatial navigation deficits in healthy older adults.

CRediT author statement

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Disclosure statement

No author involved with this research had any conflicts of interest. This work was approved by the local Ethical Committee of Université Côté d'Azur (CERNI-UCAn°2021-050) and participants provided informed consent before starting the experiment.

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Code and data availability

All raw data, codes and stimuli generated for the purpose of analyses in this paper are available via the OSF repository: https://osf.io/crne8/?view_only=7a34edf4644e49a796442388ce7ac885

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