



## Research report

# Preserved and attenuated electrophysiological correlates of visual spatial attention in elderly subjects



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## HIGHLIGHTS

- Brain signals were measured during a covert visual spatial attention task.
- Groups of young and elderly subjects performed the task equally well.
- Stimulus-locked event-related potentials were similar for both age groups.
- Alpha power and alpha lateralization were strongly reduced in elderly subjects.
- These electrophysiological changes were consistent on the single-trial level.

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## ABSTRACT

Healthy aging is associated with changes in many neurocognitive functions. While on the behavioral level, visual spatial attention capacities are relatively stable with increasing age, the underlying neural processes change. In this study, we investigated attention-related modulations of the stimulus-locked event-related potential (ERP) and occipital oscillations in the alpha band (8–14 Hz) in young and elderly participants. Both groups performed a visual attention task equally well and the ERP showed comparable attention-related modulations in both age groups. However, in elderly subjects, oscillations in the alpha band were massively reduced both during the task and in the resting state and the typical task-related lateralized pattern of alpha activity was not observed. These differences between young and elderly participants were observed on the group level as well as on the single trial level. The results indicate that younger and older adults use different neural strategies to reach the same performance in a covert visual spatial attention task.

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## 1. Introduction

Healthy aging is associated with several neural and cognitive changes. On the behavioral level, aging is associated with a decline of many cognitive functions, such as working memory and processing speed [12,19]. On the neural level, healthy elderly people show a reduction in whole brain volume, a decline in white matter integrity, and reduced resting blood flow and metabolism, with the most prominent changes in frontal regions [12,22]. Along with structural brain changes, altered patterns of task-dependent activation are observed. Overall, older adults generally show more wide-spread activation compared to younger subjects when per-

forming the same task [10,19,36]. In addition, healthy elderly individuals often show increased bilateral activation in frontal areas [3] and reduced posterior activation combined with increased anterior activation [12].

Electrophysiological measures of brain activity also indicate specific age-related neuronal changes. The resting state EEG of older adults shows a decrease of power in the slower cortical rhythms (delta, theta and alpha) and an increase of power in the faster beta and gamma rhythms [44]. Moreover, consistent with the decreased white matter integrity observed with structural imaging methods, the EEG also shows decreased connectivity, decreased modularity and decreased number of hubs with age [26].

Visual spatial attention refers to the cognitive process of directing attention to one location in external space, while ignoring other locations. Events at the attended location are processed faster [35] and more accurately [13] than events at unattended locations. Spa-

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tial attention is reflected in the amplitude of several event-related potential (ERP) components, including N1, P1 and P3, which are larger in response to stimuli occurring at attended as compared to unattended locations [8,33]. Additionally, oscillations in the alpha band (8–14 Hz) from posterior brain areas show a particular topography depending on the direction of visual spatial attention: when attention is directed to one half of the visual field, an increase in alpha power is observed over ipsilateral posterior areas, while alpha power decreases over contralateral posterior areas [23,47].

Performance on visual spatial attention tasks appears stable with increasing age [9,20,21]. However, there are indications that the neural activity underlying spatial attention changes with age. In the first place, resting-state fMRI research shows decreased connectivity within the dorsal attention network [1]. Secondly, elderly subjects who perform the Posner cueing task show an increased latency of the early ERP components P1, N1 and Nd1 [9]. In addition, the attention-related P3-component of the ERP has a reduced amplitude, increased latency and a more frontal topography in elderly as compared to young subjects [5,18,34,43]. Finally, a recent study by Hong et al. [21] showed an absence of alpha lateralization in older adults during a spatial attention task.

The traditional approach to study spatial attention-related brain signals is to collect a large number of trials and compute an average brain response over all subjects and trials. While averaging over many trials has the benefit of improving the signal to noise ratio, subtle changes in the brain responses between trials are lost. To overcome this problem, the grand average approach can be complemented by single trial analysis using machine learning techniques. It has been shown before that the direction of spatial attention can be reliably decoded from single trial ERPs [15,41] and single trial alpha lateralization [25,40]. The accuracy with which the direction of attention can be decoded is a measure of the consistency of the brain signals on the single trial level: the more consistent the brain response in every single trial, the more reliably the direction of attention can be decoded.

In this experiment, we measured spatial attention-related ERPs and alpha lateralization in young and elderly subjects. We expected to replicate the previously reported changes in the ERP (i.e. reduced amplitude, increased latency and more frontal distribution) and the absence of alpha lateralization as found by Hong et al. [21]. Apart from alpha lateralization, we also investigated the strength of overall occipital alpha power, because we hypothesized that the absence of alpha lateralization in elderly subjects may result from a decrease of alpha activity itself in the elderly brain [39,44]. In addition to alpha activity, we looked for age-related power changes in frequencies outside the alpha band to investigate whether information that is represented in the alpha band in younger subjects may shift to other frequencies in elderly subjects. To answer these questions, we compared the grand average brain signals of young and elderly subjects and used machine learning techniques to investigate the consistency of age-related changes on the single trial level.

## 2. Methods

### 2.1. Participants

Ten young participants (6 female), aged 19–29 (mean 25) years old and ten elderly participants (3 female), aged 66–76 (mean 69) years old, participated in this experiment. Subjects did not report any neurological or psychiatric abnormalities, had normal or corrected to normal vision, and did not use psychoactive medication. The experiment was approved by the ethical committee of the Faculty of Social Sciences of the Radboud University and all participants gave written informed consent prior to the experiment.

### 2.2. Materials

EEG was recorded with 64 sintered Ag/AgCl active electrodes (BioSemi, Amsterdam, The Netherlands), placed according to the international 10–20 system, at a sampling rate of 2048 Hz. Simultaneously, eye gaze was recorded with an EyeLink 1000 eyetracker (SR Research Ltd., Ontario, Canada) at a sampling rate of 1000 Hz. The subject's head was stabilized on a chin rest. Visual stimuli were presented on a 17" TFT screen with 800 × 600 pixel resolution and a refresh rate of 60 Hz.

Subjects were seated in front of a table. The screen and the eye-tracking camera were placed in the middle of the table at a distance of approximately 60 cm from the subject. A button box was placed directly in front of the subject.

### 2.3. Stimuli

A schematic representation of the stimuli is shown in Fig. 1b. A fixation cross of 1 × 1 cm (1.0° × 1.0°) was presented in the middle of the screen, with two squares 5.5 cm (5.2°) to the side and 2.2 cm (2.0°) below the fixation cross. The squares were 4.2 × 4.2 cm (4.0° × 4.0°) in size.

During trials, the color of the squares alternated between pure red, green and blue, with the color intensity depending on the experimental condition.

### 2.4. Task

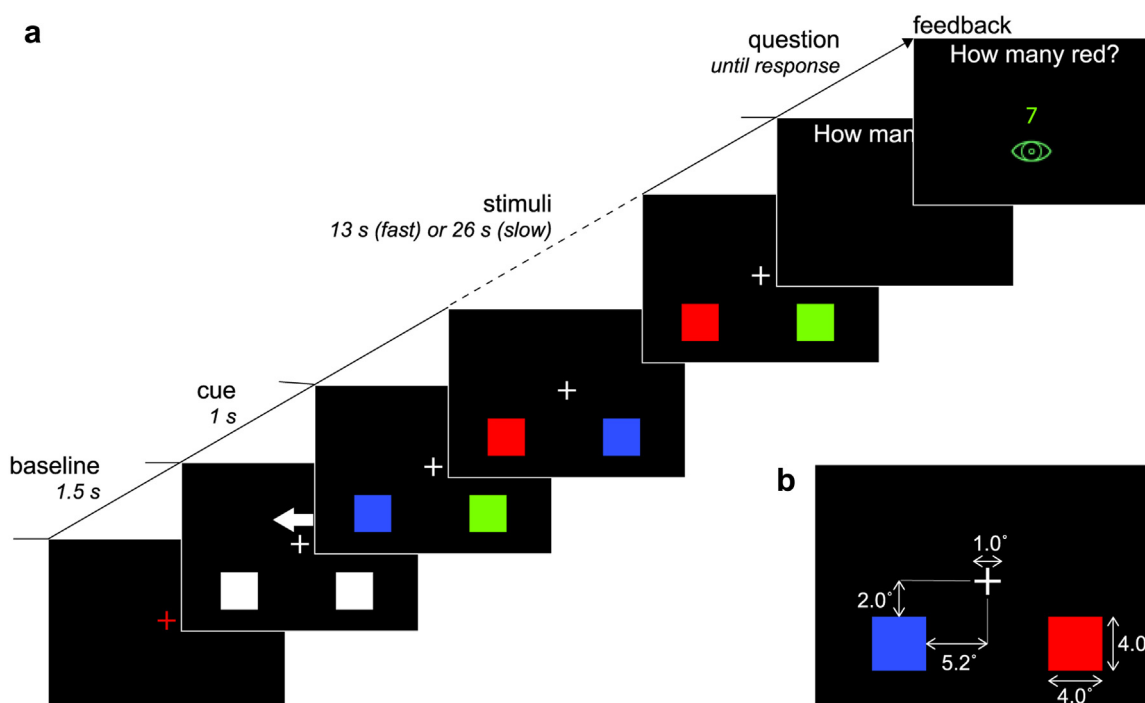
The task was designed to allow for simultaneous measurement of stimulus-locked ERPs and alpha lateralization. A schematic overview of a trial is shown in Fig. 1a. Each trial started with a baseline period, followed by an arrow pointing either to the left or to the right square for 1 s. Then the squares changed color 26 times with the time between color changes depending on the experimental condition. The subjects' task was to count the number of times the square on the side indicated by the arrow turned red. The sequences of color change on the left and right were independent from each other with the restriction that the left and right squares were never red simultaneously. In each sequence both squares turned red six, seven or eight times, with equal probability.

At the end of the trial, subjects were asked to indicate with a button press how many times the square on the indicated side had turned red, choosing from the answers 5 to 8. Although the number of red squares in a sequence never equaled 5, this alternative was presented in case subjects missed one of the red color changes. While subjects performed the task, their eye gaze was monitored online. In an attempt to maintain subjects' motivation level, points were awarded at the end of each trial, subjects received points for a correct answer and for maintaining eye gaze on the fixation cross throughout the trial.

Participants first completed a practice block, followed by 30 trials for each of the four experimental conditions, divided into six blocks of approximately 10 min.

### 2.5. Conditions

Age is associated with a decline in sensitivity and speed of visual perceptual processing [16,22]. Therefore, we included four conditions with different color intensity and speed, so that we would be able to match the behavioral performance of the age groups by selecting the conditions on which the performance was most similar. The conditions consisted of the four possible combinations of two levels of color intensity and two rates of color change. Each subject participated in all conditions, with the order of conditions counterbalanced across subjects.



**Fig. 1.** Schematic overview of the experimental design. a) Trial timeline. Each trial started with a 1-s baseline, followed by an arrow cue indicating which side should be attended. Subsequently, the color of the square alternated between red, blue and green 26 times, with an SOA of 0.5 s in the fast conditions and 1 s in the slow conditions. At the end of the trial subjects were asked to report how many red squares they had counted on the indicated side and they received feedback about their answer and eye gaze. b) Stimulus display. Size and positioning of the stimuli on the computer screen. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In conditions with bright colors, the colors had the maximum possible brightness while the perceived brightness of different colors was approximately equal (RGB values [158 0 0] for red, [0 112 0] for green, and [0 0 255] for blue). In conditions with dim colors, half of the maximum brightness was used (RGB values [79 0 0] for red, [0 56 0] for green, and [0 0 128] for blue).

In conditions with fast color changes, the time between two successive color changes was 500 ms, whereas in conditions with slow color changes, the time between color changes was 1000 ms. For the fast conditions, all 30 trials were presented in one block, but since trials lasted twice as long in the slow conditions, those trials were presented in two blocks of 15 trials with a short break in between.

## 2.6. Eye gaze analysis

The position of subjects' gaze was analyzed after each trial. Trials were excluded from further analysis when gaze position deviated more than  $3^\circ$  from the fixation cross in any direction for longer than 50 ms.

For three young and two elderly participants, a large number of trials were rejected because of a single short eye movement during that trial. For these participants, eye gaze was reanalyzed offline, checking for each stimulus if gaze position was on the fixation cross from 200 ms before to 600 ms after stimulus onset. From each trial, only the time windows around individual stimuli where eye gaze deviated from fixation were excluded from analysis.

For three additional elderly participants, it was not possible to get accurate eyetracker data at all, because their glasses were not compatible with the eyetracker. To assess if these subjects had excessive eye movements, we compared the variance in frontal channels FP1 and FP2 for those subjects with the variance in the same two channels for the other subjects. These channels were chosen as they showed the highest sensitivity to the ocular artifact. The

EOG variance of one subject without gaze monitoring exceeded 4 times the standard deviation of the variance of the other subjects, indicating many eye movements during the trials. Therefore this subject was excluded from further analysis. The EOG variance of the other subjects without gaze monitoring was within less than 0.3 standard deviations of the variance of the other subjects. We therefore assumed these subjects did not make significantly more eye movements than the subjects with gaze monitoring and included them in the analysis.

## 2.7. EEG preprocessing

The raw EEG data was sliced into trials containing 24 stimuli (the first and last stimulus were excluded from analysis because part of the event-related potential window fell outside the stimulation period). The data was downsampled to 256 Hz and re-referenced to the common average, that is the mean over all electrodes. A channel was marked as bad if the power in this channel was more than 3.5 standard deviations above the average channel power. Similarly, a trial was marked as bad if the power in this trial over all channels was more than 3.5 deviations above the average trial power. Bad trials and channels were removed, and the data re-referenced to the new common average to compensate for the removed channels. To ensure data from all subjects had the same set of channels available removed channels were re-constructed using spherical spline interpolation [32]. From that point, there were separate analysis pipelines for analyzing ERPs and alpha lateralization.

For ERP analysis, the sliced data was linearly detrended and an FFT bandpass filter for frequencies between 0.5–12 Hz was applied [14]. For classification analysis only, the data was further down-sampled to 32 Hz in order to reduce the computational load (as 32 Hz is more than 2 times the maximum filter signal of 12 Hz, a higher sampling rate is unnecessary). Each trial was then subsliced

into (possibly overlapping) epochs from 0 to 800 ms after onset of each of the 24 stimuli. Finally, the small epochs were again linearly detrended.

Alpha lateralization was analyzed by computing a spherical spline current source density (CSD) transform (which is equivalent to a scalp laplacian) of the data from 0.5–6.5 s after stimulus onset, using the CSD toolbox of Kayser and Tenke [24]. The data was subsliced into windows of 2 s and for each window the power spectrum was computed using the Welch method with six overlapping windows of 1 s. For classification analysis only, the result was normalized such that each frequency's average power over all trials was 1 and log transformed.

## 2.8. Single trial classification

Responses to transient stimuli were spatially whitened to remove cross correlation between channels [14]. Only responses to red squares on the attended side (targets) and unattended side (non-targets) contain information about the direction of attention. In order to balance the number of targets and non-targets and save computational load, only these responses were used to train the classifier, but the classifier was tested on all responses. A regularized linear logistic regression classifier (rLLR) was trained to separate the two classes, with ten-fold cross validation to set the L2 regularization strength. Classification performance was calculated for this binary problem, resulting in 24 decision values per trial (one for every stimulus). Thus, in this classification procedure we separated responses to target colors from responses to non-target colors, however we are interested in separating attention directed to the left from attention directed to the right. To determine whether attention was directed to the left or to the right, we combined the 24 decision values within each trial as follows. Every trial has a codebook, which is a matrix of 2 sides (left and right) by 24 stimuli that indicates for each side-stimulus-combination whether it is a target stimulus (red square, codebook value 1) or not (any other color, codebook value 0). At the end of the trial the 24 decision values for the target versus non-target classification were multiplied by the codebook and summed, resulting in a decision value for right-sided attention and one for left-sided attention. The side with the highest summed decision value was selected.

For classifying alpha lateralization, we used the power in the frequencies from 8 to 14 Hz. All electrodes were included in the analysis. Again an rLLR classifier was trained with ten-fold cross validation and classification performance was calculated for the binary problem.

On average, subjects completed as many trials with left-sided attention as trials with right-sided attention, resulting in a dataset with balanced classes.

## 2.9. Statistical analyses

For all statistical tests, the significance level was set to 0.05. For MANOVAs and *t*-tests the SPSS Statistics 21.0 software package was used, while the cluster-based permutation tests were performed with FieldTrip [31].

### 2.9.1. Stimulus parameters

We performed four different tests to compare the four combinations of different stimulus parameters. First, a  $2 \times 4$  mixed between-within MANOVA was performed on behavioral accuracies with group (young and elderly) and condition (fast bright, fast dim, slow bright and slow dim) as factors. In addition, F-statistic within-subject cluster-based permutation tests were used to compare target – non-target ERP difference waveforms and power spectra of the four conditions within each age group. Finally, classification accuracies in the four conditions were compared using a  $2 \times 4 \times 2$

mixed between-within MANOVA on the classification accuracies with group (young or elderly), condition (fast bright, fast dim, slow bright, slow dim) and brain response (ERPs or alpha lateralization) as factors. Only the target versus non-target ERP cluster test for young participants showed a significant difference between conditions, at 100–220 ms and 590–710 ms after stimulus onset (cluster *p*-values < 0.025). As these differences were not in the P3 time range of interest and none of the other tests were significant, we collapsed the data over conditions for further analysis.

### 2.9.2. Behavioral performance

For comparing behavioral performance between young and old participants and across conditions, we performed an independent samples *t*-test on behavioral accuracies.

### 2.9.3. Event-related potentials

We compared the ERPs to target (red squares) and non-target (blue or green squares) for each subject group (young or elderly) using *t*-statistic within-subjects cluster-based permutation tests [28].

### 2.9.4. Power spectra and power modulation

The average power spectra of young and elderly participants were compared using a between-groups cluster-based permutation test.

Power modulation is calculated by subtracting the power spectrum of trials with rightwards attention from the power spectrum of trials with leftwards attention and dividing the difference by the sum of the two power spectra [37]. The average power modulation spectra of young and elderly participants were compared using a between-groups cluster-based permutation test.

### 2.9.5. Classification of left vs right-sided attention

In order to compare the accuracy of distinguishing between left and right-sided attention, we performed a  $2 \times 2$  mixed between-within MANOVA on the classification accuracies with group (young or elderly) and brain response (ERPs or alpha lateralization) as factors.

## 3. Results

### 3.1. Number of trials

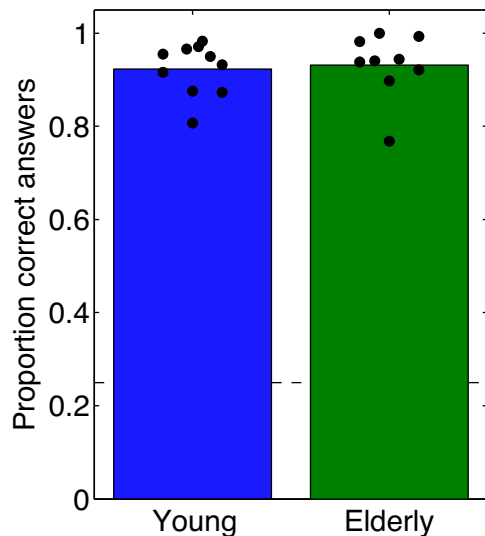
After artifact rejection and rejection of trials where eye gaze deviated from fixation, on average 109 trials remained for the young subjects and 108 trials for the elderly subjects. The number of trials determines the confidence interval around the chance level of the classification procedure [29]. Given the number of trials in this experiment, classification accuracies of 0.59 and higher are considered significantly better than chance level.

### 3.2. Behavioral performance

The behavioral performance on the counting task is shown in Fig. 2. On average, subjects counted the correct number of red squares in more than 90% of the trials. There was no significant effect of age group on behavioral performance.

### 3.3. ERP results

Grand average ERP responses to target and non-target stimuli are shown in Figs. 3 and 4. The cluster-based permutation tests revealed a significant P3 modulation in all conditions for both young and elderly subjects. The P3 appears somewhat smaller, broader and more frontal for elderly subjects as compared to the

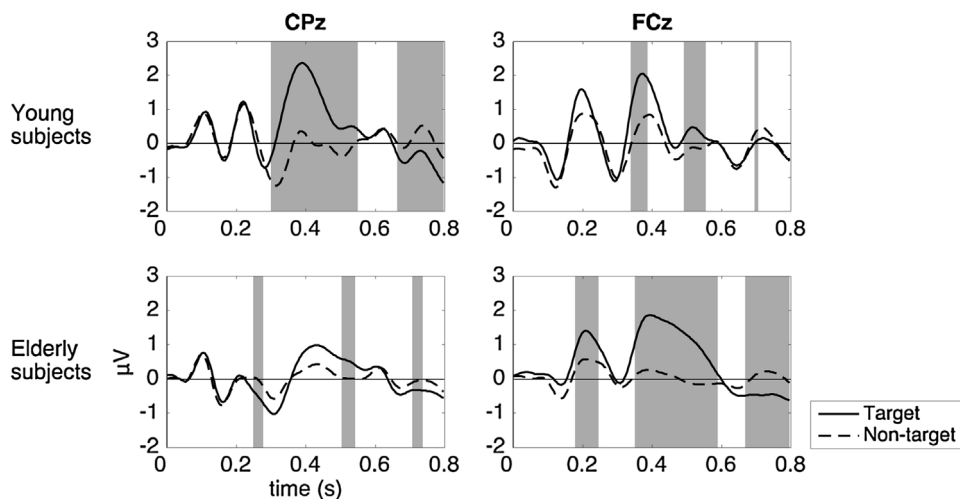


**Fig. 2.** Behavioral performance on the task. Bars show the proportion of trials in which the correct number of red squares was reported. Dots show the accuracies of individual subjects. Since subjects were offered four answer alternatives, chance level is at 25%, indicated with the dashed line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

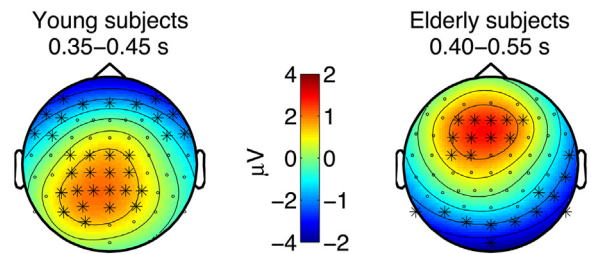
young subjects, a finding that is in accordance with existing literature [5,18,34,43]. In elderly subjects, there is also a significant difference between target and non-target responses in the P2 component.

#### 3.4. Power spectra during baseline and active task

A clear occipital alpha peak around 10 Hz is visible in the grand average power spectrum of the young, but not the older subjects (Fig. 5). While the spectrogram of the young subjects has a characteristic 1/f shape, power in the low frequencies is reduced in the elderly subjects, resulting in a flatter power spectrum. This was confirmed by a cluster-based permutation test, which revealed that power in the frequencies 1–14 Hz was significantly stronger in young subjects at all electrodes. No significant differences were found between the groups at other frequencies.



**Fig. 3.** Grand average ERPs. Average brain response to target stimuli (solid line) and non-target stimuli (dashed line) in each experimental condition. Shaded areas indicate significant differences. Note that as expected whilst the early responses up to about 300 ms are similar between both groups, the location of the main target/non-target distinction is both at a more frontal location (FCz) and broader in time for the elderly subjects.



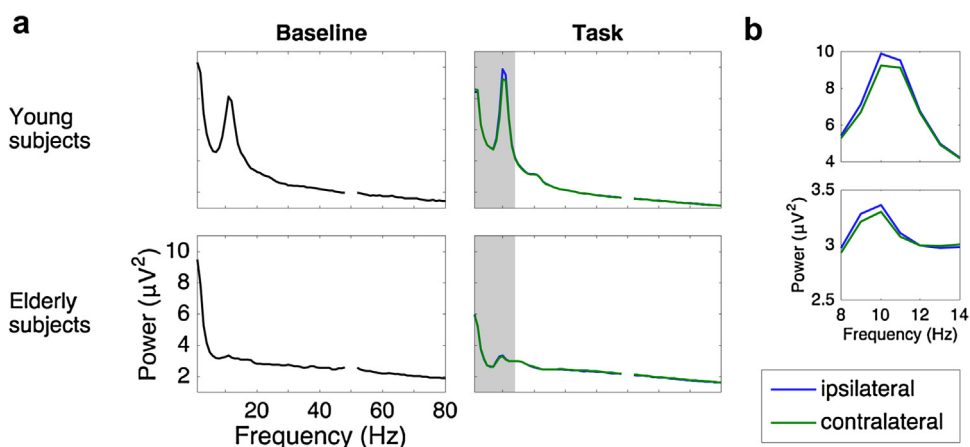
**Fig. 4.** Grand average target versus non-target differences. Average difference between target and non-target responses in each experimental condition. Asterisks indicate channels where the target – non-target difference is significant. Please note the different scales for young and elderly subjects. The significant negative difference (in blue) in frontal and occipital electrodes is likely an artifact of the common average reference. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

#### 3.5. Alpha modulation

Average task-dependent alpha modulation in young and elderly subjects is shown in Fig. 6. Alpha modulation is calculated by subtracting the power spectrum of trials with rightwards attention from the power spectrum of trials with leftwards attention and dividing the difference by the sum of the two power spectra [37]. In young subjects, power in the alpha range shows the expected ipsilateral increase and contralateral decrease in occipital electrodes. In the elderly group, the typical lateralized pattern of alpha modulation is not visible. However, this difference in alpha power modulation between young and elderly subjects is not statistically significant.

#### 3.6. Single trial classification

The direction of attention (left or right) could be reliably decoded from single trial ERPs in all young and elderly subjects (see Fig. 7a). Decoding based on alpha lateralization was less accurate, but above chance level for the majority of young subjects. For most elderly subjects, decoding based on alpha lateralization was not significantly better than chance. The group  $\times$  brain signal MANOVA showed that classification based on ERPs was significantly more accurate than classification based on alpha lateralization ( $F = 317$ ,  $p < 0.001$ , partial  $\eta^2 = 0.95$ ). This difference in performance between the two neural signatures was larger for the elderly than the young



**Fig. 5.** Grand average power spectra. a) Average power spectra for young and elderly subjects at channels O1/O2. For the power spectrum during task performance, separate lines are shown for attention ipsilateral and contralateral to the electrodes. Shaded areas indicate a significant difference between young and elderly participants. Frequencies 49–51 Hz are omitted because of line noise artifacts in these frequencies. b) Enlarged view of the power in the alpha band (8–14 Hz) of young subjects (top) and elderly subjects (bottom). Please note the different scales for young and elderly participants. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

subjects ( $F = 10.6$ ,  $p < 0.05$ , partial  $\eta^2 = 0.38$ ). There was no significant effect of group on classification performance.

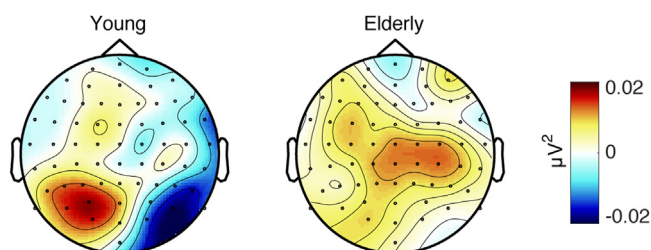
Fig. 7b and c shows the classifier weights of the ERP and alpha classifiers, respectively. As we use a regularized classifier, magnitude of the classifier weight is an indication of the importance of that feature for correct decoding. The topographical pattern of the weights is similar to the grand average electrophysiological signals shown in Figs. 4 and 6, indicating that these signals carry information about the direction of attention on the single trial level.

### 3.7. Lateralized power changes in higher frequencies in elderly subjects

In young subjects, no task-dependent lateralization is visible in frequencies higher than the alpha range. For elderly subjects, a lateralized pattern of higher frequency activity is visible in occipital and frontocentral electrodes (Fig. 8a). The modulation of power at frequencies higher than 20 Hz is significantly stronger in elderly than in young subjects (cluster  $p$ -value  $< 0.01$ ). In addition, a classifier trained on the frequencies of 30–45 Hz can reliably decode the direction of attention in the majority of elderly, but none of the young participants (Fig. 8c). The weights of this classifier show a similar topographical pattern as the grand average power modulation (Fig. 8b), indicating that the power modulation in this frequency range is consistently present on the single trial level. It is tempting to interpret these results as some form of compensatory activity in the elderly. However, given the location of the effect and the fact that this pattern persists up to frequencies of 400 Hz, we strongly suspect that this reflects muscle rather than brain activity [46].

## 4. Discussion

In this experiment, we investigated spatial attention-related ERPs and occipital alpha activity in younger and elderly subjects. In this relatively easy task, both groups performed at ceiling level. But while ERP responses to targets and non-targets were similar for both age groups, alpha power and alpha lateralization were significantly reduced in older adults. Our results are in line with previous research on age-related changes in the ERP [5,9,18,34,43] and in alpha lateralization [21], even with a task that is different from previous studies. To the latter case we can add that not just alpha lateralization, but alpha power itself is diminished in older



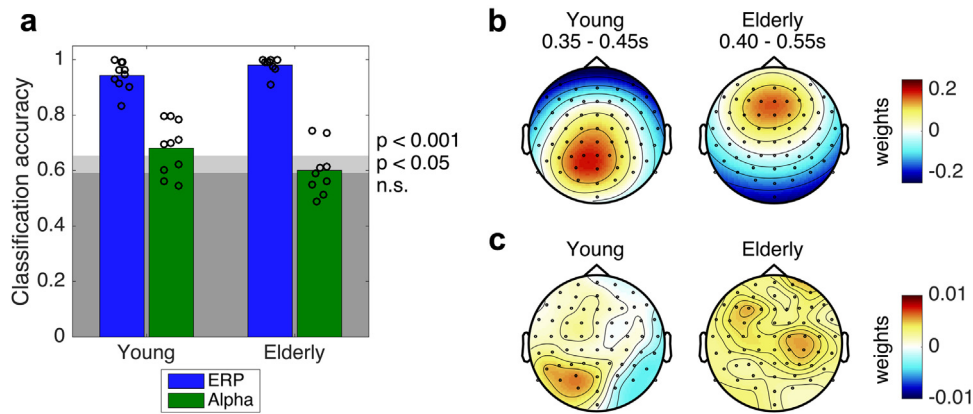
**Fig. 6.** Grand average alpha modulation. Average modulation of power in the alpha frequency range (8–14 Hz) for young and elderly subjects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

adults. Finally, classification analysis indicates that the direction of attention can be reliably decoded from single trial ERPs in both age groups, but decoding based on alpha lateralization is compromised in elderly subjects.

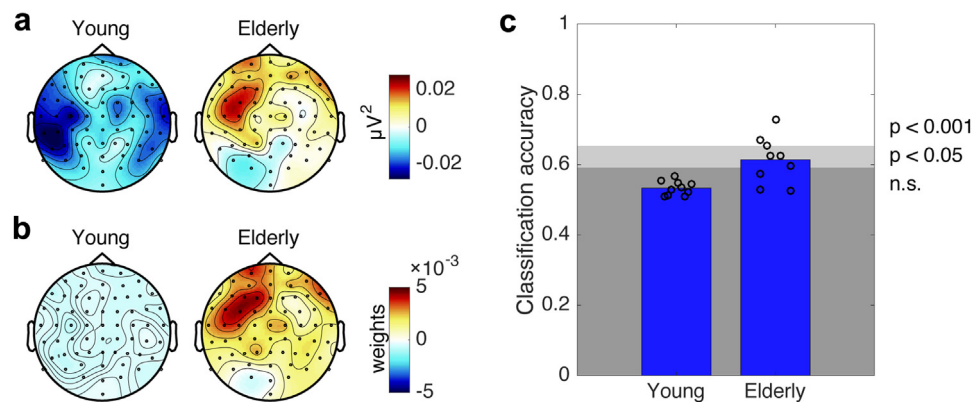
In contrast to the young subjects, elderly subjects demonstrated task-related lateralized power modulation at higher frequencies. This pattern of activity was consistently present on the single trial level. Although this might suggest a form of compensatory activity in the elderly, chances are high that this is muscle rather than brain activity.

Our results may be interpreted in light of the attention network theory of Corbetta and Shulman [7,6]. Based on a large number of primarily fMRI studies, these authors identified two separate neural networks involved in attention: a dorsal and a ventral network. The goal-driven dorsal attention network exerts top-down control over sensory areas to bias the processing of incoming stimuli. It has been shown that the dorsal attention network controls visual spatial attention through alpha lateralization in the visual cortex [4]. The ventral attention network on the other hand is responsible for the more stimulus-driven type of attention and is important for the reorienting of attention. The P3 component of the ERP has been reliably associated with the ventral attention network [6]. Therefore, the results of our study could indicate that age may have stronger effects on the dorsal than the ventral attention network. In line with this is the observation that functional connectivity of the dorsal system in resting state is decreased in elderly participants [1].

While elderly subjects showed diminished alpha activity in occipital electrodes, we did observe some lateralized activity in the alpha range in right central electrodes. A similar pattern of



**Fig. 7.** Classification results. a) Decoding accuracies. Bars show the proportion of trials in which the direction of attention could be correctly decoded from ERPs or lateralized alpha. Circles show the decoding accuracies for individual subjects. Grey and white areas indicate whether decoding accuracy is significantly better than chance level. b) Weights of the ERP classifier in the P300 time window. c) Weights of the alpha classifier. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 8.** Task-related power modulation in higher frequencies. a) Average modulation of power in the 30–45 Hz frequency range for young and elderly subjects. Power modulation is calculated by subtracting the power spectrum of trials with rightwards attention from the power spectrum of trials with leftwards attention and dividing the difference by the sum of the two power spectra [37]. b) Average weights of a classifier trained on frequencies 30–45 Hz. c) Decoding accuracies of a classifier trained on frequencies 30–45 Hz. Bars show the proportion of trials in which the direction of attention could be correctly decoded. Circles show the decoding accuracies for individual subjects. Grey and white areas indicate whether decoding accuracy is significantly better than chance level. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

activity, though less focal than in our data, can be seen in the data of Hong et al. [21]. The pattern is also visible in the classifier weights in Fig. 7c, suggesting that it is consistently present on the single trial level. This finding may be comparable to the fMRI-based Posterior–Anterior Shift in Aging (PASA) hypothesis [11]: the common observation that elderly subjects show more activity in frontal brain areas as compared to younger subjects when performing the same task. A similar effect in EEG was reported by Walhovd et al. [45]. Importantly, compensatory activity can indicate either the recruitment of new networks that were previously not used for a task or an increase in the engagement of networks that previously played a much smaller (but nevertheless functional) role in the achievement of the same task [42]. In this study, we cannot distinguish between these two possible mechanisms. In any case, the fact that the single trial classification accuracies of the alpha lateralization classifier are lower for elderly subjects indicates that this right central pattern of activation in the elderly is not as strongly associated with the direction of attention as the occipital alpha lateralization in the young.

Together, the results of our study seem to imply that the young and elderly participants used different neural strategies to complete this visual spatial attention task. Whereas the young subjects

showed attention-related changes in the P300 and in lateralized alpha activity, the latter neural signature was absent in elderly subjects. It has been shown that lateralized alpha activity is required for optimal performance across a range of different tasks [23,38]. However, in the present study, elderly subjects were able to reach the same level of performance as younger subjects without employing lateralized occipital alpha activity. There are a number of possible explanations for this result. Firstly, it could be that alpha lateralization may be necessary for some, but not all, spatial attention tasks, and that the task used in this study is an example of a situation where alpha lateralization is not required for adequate performance. In this case, the alpha lateralization that is observed in some of the subjects would be an epiphenomenon rather than a prerequisite for spatial attention. An alternative explanation could be that some subjects are able to adopt a mental strategy which achieves high task performance without alpha lateralization, for example by relying more strongly on stimulus-driven than top-down attention. Finally, some subjects might be able to employ spatial attention without active alpha lateralization, that is, for these subjects spatial attention would not be reflected in alpha lateralization, but in some other unknown neural signature. The observed difference in alpha lateralization between younger and older adults could indicate a

shift from one neural strategy to another across the lifespan. However, our results indicate that the neural signatures associated with spatial attention are not purely dependent on age, since although on average the younger subjects showed a lateralized pattern of alpha modulation, some individual subjects did not, as can be seen in Fig. 7. Conversely, in the elderly group, where alpha lateralization was absent on average, there were participants who did show lateralized alpha activity.

Occipital alpha activity as well as P300 amplitude have been used to control brain-computer interfaces (BCIs) [2,15]. Most of this BCI research has been done on young subjects. Our results clearly indicate that with increasing age, people will likely retain the ability to control P300-based BCIs, but the performance of alpha-based BCIs [2,40] or neurofeedback-based cognitive rehabilitation systems [27] may decline when users get older. This should be an important consideration in selecting a BCI or neurofeedback application for an elderly user.

In conclusion, the present study indicates that younger and older adults rely on different neural mechanisms to perform a relatively easy covert visual spatial attention task. Whereas behavioral performance and evoked responses were similar for both age groups, the pattern of lateralized occipital alpha activity that is commonly observed in young subjects was absent in nearly all elderly subjects. Future research is needed to understand the functional role of lateralized alpha activity across different age ranges and experimental tasks, and to investigate the meaning of individual differences observed within groups of participants.

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