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Alpha modulation in younger and older adults during distracted encoding

Syanah C. Wynn[1,2,3] | **Erika Nyhus**[2,3] | **Ole Jensen**[4]

[1]Donders Institute for Brain, Cognition and Behaviour, Radboud University, Nijmegen, The Netherlands

[2]Department of Psychology, Bowdoin College, Brunswick, Maine, USA

[3]Program in Neuroscience, Bowdoin College, Brunswick, Maine, USA

[4]Centre for Human Brain Health, School of Psychology, University of Birmingham, Birmingham, UK

Correspondence
Syanah C. Wynn, Bowdoin College, Brunswick, ME, USA.
Email: swynn@bowdoin.edu

Abstract

To successfully encode information into long-term memory, we need top-down control to focus our attention on target stimuli. This attentional focus is achieved by the modulation of sensory neuronal excitability through alpha power. Failure to modulate alpha power and to inhibit distracting information has been reported in older adults during attention and working memory tasks. Given that alpha power during encoding can predict subsequent memory performance, aberrant oscillatory modulations might play a role in age-related memory deficits. However, it is unknown whether there are age-related differences in memory performance or alpha modulation when encoding targets with distraction. Here we show that both older and younger adults are able to encode targets paired with distractors and that the level of alpha power modulation during encoding predicted recognition success. Even though older adults showed signs of higher distractibility, this did not harm their episodic memory for target information. Also, we demonstrate that older adults only modulated alpha power during high distraction, both by enhancing target processing and inhibiting distractor processing. These results indicate that both younger and older adults are able to employ the same inhibitory control mechanisms successfully, but that older adults fail to call upon these when distraction is minimal. The findings of this study give us more insight into the mechanisms involved in memory encoding across the lifespan.

KEYWORDS

alpha power, attention, EEG, episodic memory, inhibition, oscillations

1 | INTRODUCTION

In order to attentively encode new information, we have to guide processing resources toward the encoding of target stimuli. When targets are attended, top-down control facilitates target-related activity, increasing the efficacy of memory encoding via the medial temporal lobe (Chun & Turk-Browne, 2007; Uncapher & Rugg, 2009; Uncapher & Wagner, 2009; Xue et al., 2012). This top-down control is supported by a frontoparietal attentional network that selectively modulates

Abbreviations: ANOVA, analysis of variance; CMS, common mode sense; cPMI, combined power modulation index; d', d-prime; dB, decibel; DRL, driven right leg; DS, distractor; EEG, electroencephalography/ electroencephalogram; EOG, electro-oculography/ electrooculogram; GLM, general linear model; HD, high distraction; Hz, hertz; ICA, independent component analysis; IDT, inhibition-deficit theory; LAD, lateralized alpha power; LD, low distraction; LH, left hemisphere; M, mean; MMSE, mini-mental state examination; ms, millisecond; oct, octave; P, power; PMI, power modulation index; RH, right hemisphere; RM ANOVA, repeated measures analysis of variance; SD, standard deviation; TFR, time-frequency representation; Z, z-score.

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sensory neuronal excitability, mediated by long-range alpha (8–14 Hz) oscillations (Corbetta & Shulman, 2002; Maunsell & Treue, 2006; Lenartowicz et al., 2016; Markant et al., 2015; Sadaghiani et al., 2012; Uncapher & Wagner, 2009; Wang et al., 2016). Increased neuronal excitability needed for goal-oriented stimulus processing, is reflected in decreased alpha power over these sensory areas (Bauer et al., 2014; Thut et al., 2006). Apart from attending to targets, there is often a need to concurrently inhibit task-irrelevant information. This can be achieved through an increase in alpha power over sensory areas involved in processing distractor information, decreasing neuronal excitability (Jensen & Mazaheri, 2010; Bonnefond & Jensen, 2012; Janssens et al., 2018). Therefore, effective modulation of alpha power could be important for the encoding of new information into long-term memory.

It has been suggested that with age, our ability to successfully minimize the influence of distraction declines. Specifically, according to the inhibition-deficit theory (IDT), age-related memory deficits are caused by a failure to inhibit irrelevant information, at the expense of attending to relevant information mediated by top-down control (Hasher et al., 1988; Kane et al., 1994; Li et al., 1998; Lustig et al., 2007). While studies in favor of the IDT have reported that older adults are less capable of inhibiting distracting information (Devitt et al., 2016; Mund et al., 2012; Sander et al., 2011, 2012; Wais et al., 2012; Zanto et al., 2010), others have suggested that episodic memory is not harmed by this increase in distractibility (Aslan et al., 2007; Fernandes & Moscovitch, 2003; Zellner & Bauml, 2006). Therefore, it is still unclear whether age-related episodic memory decline is due to inhibitory deficits. The majority of studies in the field have defined "episodic memory" as the long-term memory for the items encoded during an experimental session. As such, the episodic memories are specific to the experimental "episode." We will use this definition throughout this paper.

Since aberrant modulations of alpha power have been related to inhibitory failure (Ellis et al., 2017; Hale et al., 2009; ter Huurne et al., 2013), it is of interest to investigate age differences in alpha power modulation. In younger adults, decreases in alpha power during stimulus presentation have been linked to successful episodic memory encoding, possibly by allowing for more information to be encoded by distributed neuronal firing (Hanslmayr et al., 2012, 2016; Hanslmayr & Staudigl, 2014; Klimesch et al., 1999; Molle et al., 2002; Noh et al., 2014). To the best of our knowledge, there are only two recent studies that have compared encoding-related alpha activity in younger and older adults (Sander et al., 2020; Strunk & Duarte, 2019). Specifically, these studies investigated whether there were age differences in subsequent memory effects in alpha activity. Both studies found that encoding-related alpha power predicted later memory performance to the same extent in both age groups (Sander et al., 2020; Strunk & Duarte, 2019). This suggests that older adults have no problem modulating their alpha power when no distracting information is present during encoding.

When investigating inhibition-related age differences, it is important to know what happens when suppression of distractors is necessary for optimal task performance. Studies that examine age effects in relation to distraction, often utilize attention or working memory tasks. Results from these studies demonstrate that older adults show less alpha power modulation when top-down attention is required to inhibit distraction (Hong et al., 2015; Leenders et al., 2018; Rogers et al., 2018; Vaden et al., 2012; Werkle-Bergner et al., 2012). For instance, Leenders et al. (2018) showed that older adults have inhibitory deficits during working memory retention. Participants performed a lateralized working memory task and the results showed that during the retention period, older adults displayed less alpha power modulation than younger adults. Interestingly, these effects in oscillatory activity were found in the absence of behavioral differences between the two age groups. This indicates that inhibitory mechanisms might differ between younger and older adults, but do not always correlate with behavioral effects.

Fewer studies have focused on alpha modulation in relation to the encoding of distractors in episodic memory. Studies in younger adults have shown that when instructed to ignore a stimulus, alpha power increases in order to suppress further encoding (Jiang et al., 2015; Park et al., 2014). Specifically, Jiang et al. (2015) showed that during stimulus encoding, alpha power increased in the areas processing distractor information. Furthermore, they showed that participants who successfully modulated alpha power during encoding, had better memory for the target stimuli. A study by Werkle-Bergner et al. (2012) investigated episodic encoding in both younger and older adults in a paradigm involving distractors. However, they did not analyze how the alpha power modulation during encoding was related to later episodic memory. Therefore, it remains an open question of whether there are differences in encoding-related alpha power modulation between younger and older adults when distraction is present.

In the current study, younger and older adults performed a visual lateralized encoding task to explore the role of alpha modulations in recognition memory. Distracting information was presented in the unattended hemifield, while EEG was recorded throughout the encoding session. This experimental design allowed us to investigate age-related differences in both the capability to encode information under distracting conditions and the level of alpha modulation. We hypothesized that the level of alpha modulation during encoding would show a positive correlation with later recognition. Given the reports of atypical alpha power modulations in older adults in non-episodic memory tasks (Hong et al., 2015; Leenders et al., 2018; Rogers et al., 2018; Werkle-Bergner et al., 2012), aberrant alpha power modulations might also be expected here. Nevertheless, the reports on alpha modulation during

episodic memory not changing with age (Sander et al., 2020; Strunk & Duarte, 2019) and the suggestion that the IDT does not hold for episodic memory (Aslan et al., 2007; Fernandes & Moscovitch, 2003; Zellner & Bauml, 2006), make it is difficult to make a clear hypothesis regarding the age-related effects on alpha power modulation during memory encoding.

2 | METHODS

2.1 | Participants

Thirty-one older and 30 younger adults participated in this study, recruited through local advertising and the Radboud Research Participation System. All had a normal or corrected-to-normal vision, were right-handed, native Dutch speakers, non-smokers, and were free from any self-reported neurological or psychiatric conditions. Informed consent was obtained from all participants, who all received ten Euros per hour for participation. Of these 61 participants, two participants were excluded from the experiment due to inadequate adherence to test instructions. Data from the remaining 29 older adults (16 women, $M_{age} = 68.4$, $SD_{age} = 4.7$) and 30 younger adults (24 women, $M_{age} = 22.0$, $SD_{age} = 3.4$) were analyzed. The study was approved by the local ethics committee of the faculty of social sciences of the Radboud University. All older participants scored within the normal range on the Dutch version of the Mini-Mental State Examination (MMSE; $M = 29.10$, $SD = 0.96$) (Folstein et al., 1975), indicating the absence of any major neuropsychiatric disorders.

2.2 | Stimuli

The stimulus material consisted of 990 (500 × 281 pixels) colored images of natural or man-made objects that were selected from internet databases (http://www.morguefile.com and http://www.flickr.com). Stimuli were presented against a grey background on a personal computer screen with a 21-inch monitor (1920 × 1,080 pixels, 60 Hz refresh rate). Stimulus presentation and the recording of responses were attained using MATLAB (v2015b, MathWorks Inc., Natick MA) in combination with Psychophysics Toolbox extensions (v3.0.14) (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007).

2.3 | Procedure

Upon arrival at the laboratory, all volunteers were screened for eligibility to participate in EEG studies and the older adults completed the MMSE. After this screening, participants performed an eye movement localizer task, where they fixated their eyes on specific locations on the screen. Electrooculography (EOG) recordings during this task were used to identify saccades in later data preprocessing.

In the intentional encoding phase, each of the 396 trials started with one-second centrally presented fixation cross, followed by a one-second directional cue. This cue predicted the location of the upcoming target picture, with an arrow pointing to the left or right (see Figure 1). Thereafter, two pictures were presented bilaterally for one second (visual angel of 5.71° horizontal and 3.27° vertical, see Figure 1). At the uncued location, a colored image of a natural or man-made object (high-distraction condition) or a blurry picture (low-distraction condition) was presented. This blurry picture was the average of 10 colored pictures, which was held constant over trials and participants (see Figure 1). At cue presentation, participants were instructed to covertly direct their attention to the cued hemifield (left or right, equal probability). During the picture presentation, participants made a semantic classification ("natural" or "man-made") regarding the picture on the attended location (see Figure 1). Participants were instructed to keep their eyes on the fixation cross throughout the trial. There were 264 trials in the high-distraction and 132 trials in the low-distraction condition.

In the test phase, all 990 trials started with one-second centrally presented fixation cross, followed by a 1.5 s centrally presented picture. During the picture presentation, participants made an old/new judgment. Participants were instructed to respond "old" to all items encountered during encoding; the targets, and distractors. There were 264 cued pictures from the high-distraction condition ($targets_{HD}$), 264 uncued pictures from the high-distraction condition (distractors), 132 cued pictures from the low-distraction condition ($targets_{LD}$), and 330 pictures that were not presented during the encoding phase (new). After the presentation of the picture, participants rated their confidence in this "old/new" decision on a 3-point scale (see Figure 1).

A practice session preceded both the encoding and retrieval phase, familiarizing participants with the upcoming task. Pictures used in these practice sessions were not used in the experimental trials. After the memory task, participants were debriefed and received compensation for participation. The total duration of the experimental session was 2 hr.

The arrow keys were used to register the participants' responses. During encoding, the left arrow corresponded to "natural" and the right to "man-made" responses. During retrieval, the left and right arrows indicated "old" and "new" responses, respectively. For the confidence judgment the left arrow was used for "not sure," the down arrow for "a bit sure," and the right arrow for "definitely sure" responses. Participants were instructed to use only their left or right index finger, which was determined in a randomized and counterbalanced manner.

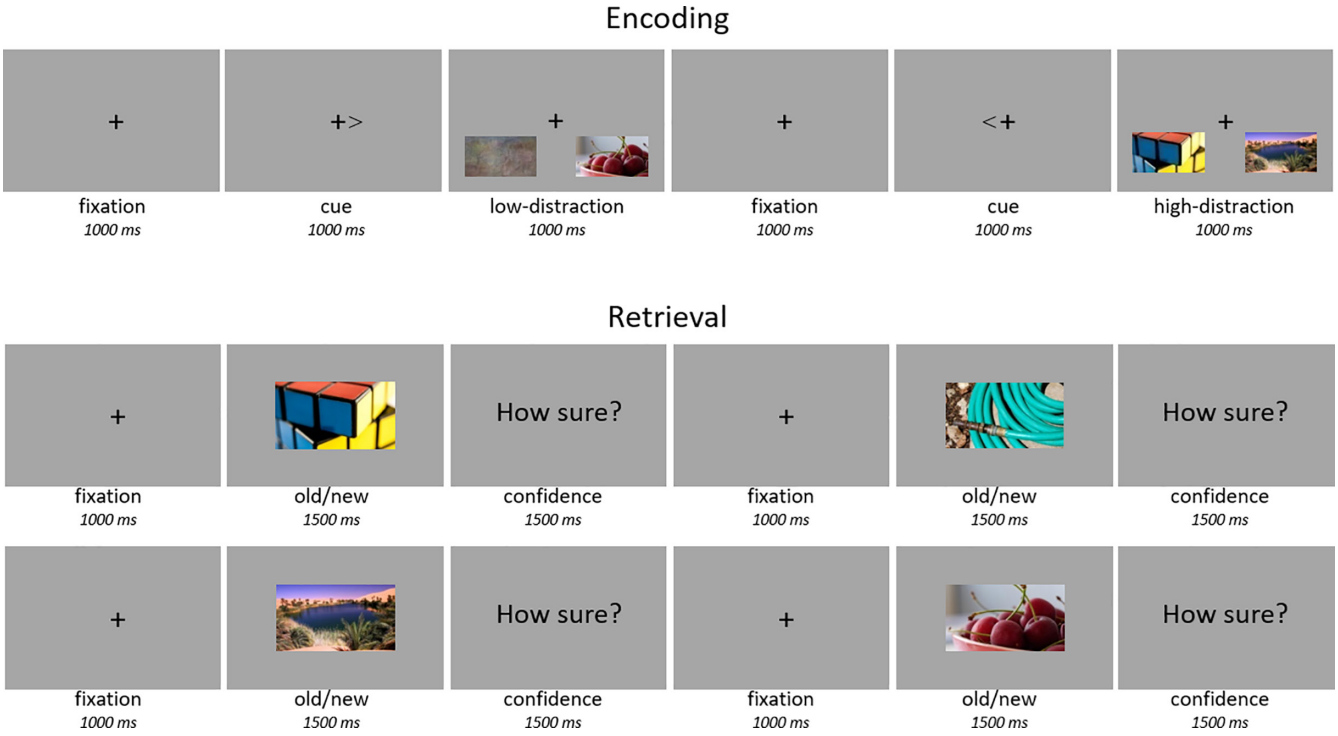

FIGURE 1 A schematic overview of the memory task. In the encoding phase, participants were instructed to fixate on the fixation cross and covertly attend the cued picture. Participants made a semantic classification ("natural" or "man-made") during picture presentation. In the retrieval phase, all pictures shown during encoding were presented again, accompanied by new pictures (foils). Participants indicated whether they saw the picture during encoding ("old" or "new") during the presentation of the pictures. Subsequently, they indicated how sure they were of this classification on a three-point scale ("not sure," "a bit sure," "definitely sure"). All responses were made with a button-press on the arrow-keys of a keyboard

2.4 | EEG acquisition

Electroencephalographic (EEG) signals were recorded and amplified with a BioSemi ActiveTwo system (BioSemi B.V., Amsterdam) from 32 Ag-AgCl-tipped electrodes, conforming to the International 10–20 System. Bipolar electrooculogram recordings were obtained from electrodes placed one cm lateral of the outer canthi, and above and below the left eye. Each active electrode was measured online with respect to a Common Mode Sense (CMS) active electrode. The combination of the CMS electrode and Driven Right Leg (DRL) passive electrode ensures that the CMS electrode stays as close as possible to the reference voltage at the analog-to-digital converter. The EEG signal was pre-amplified at the electrode to improve the signal-to-noise ratio, amplified with a 16-fold gain, and digitized at a 24-bit resolution with a sampling rate of 1,024 Hz.

2.5 | Data analyses

Data analyses were performed with the use of MATLAB (v2015b, MathWorks Inc., Natick MA) in combination with the FieldTrip toolbox (Oostenveld et al., 2011). A minimum of 15 trials per condition typically is needed to obtain stable oscillatory power estimates (Hanslmayr et al., 2009). Therefore, two additional older participants were excluded from the analyses, due to the insufficient number of trials left following artifact and saccade rejection.

2.5.1 | Behavioral analyses

Memory performance for targets and distractors was quantified by d-prime (*d'*), which was calculated using the following formulas:

$$d'_{LD} = Z(\text{hit rate}_{LD}) - Z(\text{false alarm rate})$$
$$d'_{HD} = Z(\text{hit rate}_{HD}) - Z(\text{false alarm rate})$$
$$d'_{DS} = Z(\text{hit rate}_{DS}) - Z(\text{false alarm rate})$$

Where hit rate_{LD} was the hit rate for targets from the low-distraction encoding condition, hit rate_{HD} was the hit rate for targets from the high-distraction encoding condition, and hit rate_{DS} was the hit rate for the distractors from the high-distraction condition. False alarm rate was the same in all formulas and represented the false alarm rate for all new items.

Trials in which participants failed to respond were removed from further analyses (on average 17% of encoding trials and 9% of retrieval trials). While there were no group differences during retrieval ($t(55) = 1.74$, $p = .088$), older adults failed to make a response more often than the

younger adults during encoding ($t(55) = 3.28$, $p = .002$). This suggests that the encoding task was more difficult for older adults, as compared to the younger adults. Trials containing EEG artifacts were included in the behavioral analyses. When only trials that were included in the EEG analyses were analyzed, memory performance results were comparable.

2.5.2 | EEG analyses

EEG data were re-referenced off-line to a common average reference and band-pass filtered between 0.5 and 30 Hz (roll off: 60 dB/oct). Stimulus-locked epochs (−2000 to 2000 ms) were extracted for encoding trials. In addition, trials with transient muscle or electrode artifacts were rejected based on visual inspection. With the use of independent component analysis (ICA), components that contained blinks were identified by inspecting the time course and spatial topography of all components. After blink-components were removed, epochs containing saccades were detected and removed from further analyses, with the use of an eye movement localizer task. During this localizer task, participants made saccades from the center of the screen to the center of the two locations the pictures were presented during encoding (see Figure 1).

First, per participants, the average peak to peak deflection in the horizontal EOG signal during these saccades was determined. Second, half of the value of the average peak to peak deflection was used as the participant-wise threshold value, to detect saccades in the horizontal EOG data. Therefore, the threshold indicated a saccade to approximately the location of the medial top corner of the picture. Third, encoding trials in which the horizontal EOG peak to peak values exceeded the participants' threshold value were identified. Fourth, these identified encoding trials were visually inspected for saccades. Fifth, trials with a saccade during picture presentation were removed from further analyses, leaving on average: 178 (range: 60–244) high-distraction and 87 (range: 32–126) low-distraction trials for the younger adults, and 108 (range: 36–237) high-distraction and 51 (range: 15–113) low-distraction trials for the older adults.

Time-frequency representations (TFRs) of power were calculated using Fourier analysis with sliding time-windows (1 ms steps), and Hanning tapers. Frequencies that were assessed ranged from 2 to 30 Hz, in 2 Hz steps, with a 500 ms time-window for each frequency. Consequently, the data at timepoint T represent the data from T -250 to T +250 ms. To clarify, time point 250, includes data from 0 to 500 ms and from time point 750 includes data from 500 to 1,000 ms. To have data uncontaminated by cue or stimulus processing, time-windows of, respectively, −750 to −250 ms and 250 to 750 ms were chosen for analyses.

The power modulation index (PMI) per hemisphere was computed from the grand average TFRs, using the following formula (Leenders et al., 2018):

$$\mathrm{PMI} = \frac{P_{\mathrm{left}} - P_{\mathrm{right}}}{P_{\mathrm{left}} + P_{\mathrm{right}}}$$

P_{left} is the power within a hemisphere of a given frequency band in the "attend left" encoding trials and P_{right} is the power within a hemisphere in the "attend right" encoding trials. For each hemisphere, positive PMI values indicate higher power when attending to the left hemifield as compared to the right, whereas negative values indicate the opposite. Assuming larger alpha power ipsilateral to the target location, positive PMI values are expected in the left hemisphere and negative values in the right hemisphere. To summarize the modulations in both hemispheres, a combined PMI (cPMI) measure was calculated by considering the average PMI of the right hemisphere and subtracting it from the average PMI of the left hemisphere. Positive cPMI values indicated effective modulation in the hypothesized direction.

To investigate the effect of memory condition on ipsilateral and contralateral alpha power relative to the target, the following formulas were used:

$$\mathrm{LAD}_{\mathrm{ipsi}} = \left[\frac{\left(\alpha_{\mathrm{LH}}^{\leftarrow \mathrm{HD}} - \alpha_{\mathrm{LH}}^{\leftarrow \mathrm{LD}}\right)}{\left(\alpha_{\mathrm{LH}}^{\leftarrow \mathrm{HD}} + \alpha_{\mathrm{LH}}^{\leftarrow \mathrm{LD}}\right)} + \frac{\left(\alpha_{\mathrm{RH}}^{\rightarrow \mathrm{HD}} - \alpha_{\mathrm{RH}}^{\rightarrow \mathrm{LD}}\right)}{\left(\alpha_{\mathrm{RH}}^{\rightarrow \mathrm{HD}} + \alpha_{\mathrm{RH}}^{\rightarrow \mathrm{LD}}\right)} \right] / 2.$$

$$\mathrm{LAD}_{\mathrm{contra}} = \left[\frac{\left(\alpha_{\mathrm{RH}}^{\leftarrow \mathrm{HD}} - \alpha_{\mathrm{RH}}^{\leftarrow \mathrm{LD}}\right)}{\left(\alpha_{\mathrm{RH}}^{\leftarrow \mathrm{HD}} + \alpha_{\mathrm{RH}}^{\leftarrow \mathrm{LD}}\right)} + \frac{\left(\alpha_{\mathrm{LH}}^{\rightarrow \mathrm{HD}} - \alpha_{\mathrm{LH}}^{\rightarrow \mathrm{LD}}\right)}{\left(\alpha_{\mathrm{LH}}^{\rightarrow \mathrm{HD}} + \alpha_{\mathrm{LH}}^{\rightarrow \mathrm{LD}}\right)} \right] / 2.$$

In these formulas, α stands for alpha power, LD for low distraction, HD for high distraction, RH for the right hemisphere, LH for the hemisphere, ←for target left, and →for target right. Accordingly, $\alpha_{\mathrm{RH}}^{\leftarrow \mathrm{LD}}$ represents right hemispheric alpha power, while attending left in the low-distraction condition. These formulas give the normalized mean lateralized alpha power difference (LAD) between the high- and low-distraction condition, for the ipsi- and contralateral hemisphere. Where positive $\mathrm{LAD}_{\mathrm{ipsi}}$ values represent an increase in ipsilateral alpha power from the low- to the high-distraction condition, and negative $\mathrm{LAD}_{\mathrm{contra}}$ values represent a decrease in contralateral alpha power from the low- to the high-distraction condition. Both values are with respect to the location of the target.

2.5.3 | Statistical analyses

Group effects on the behavioral level were tested using general linear models (GLMs), with age-group as the

between-subject factor and memory performance and confidence as dependent variables. Effect sizes (partial eta-squared; η_p^2) were computed for all analyses. When a GLM was significant, post hoc tests were performed using Fisher's least significant difference procedure.

To assess differences in alpha power between the younger and older adults, the analyses focused on sensors and frequencies that were sensitive to the experimental attentional manipulation. To select the region and frequencies of interest, a cluster-based nonparametric permutation test was performed (Maris & Oostenveld, 2007). TFRs of all "attend left" trials and all "attend right" trials were pooled together across participants. To identify sensors and frequencies that reliably distinguished between the attentional conditions without any contribution from encoding-related processes, we analyzed the cue window (−750 to −250 ms, relative to stimulus onset). In the cue window, participants were instructed to covertly direct their attention to the cued hemifield, but encoding-related processes were expected to be minimal. To be able to select the region and frequencies of interest, all sensors and frequencies were included in the analyses. For every sample (sensor by frequency pair), the "attend left" and "attend right" conditions were compared by means of a t-value. All samples with an α-value smaller than 0.05 were selected and clustered on the basis of spatial and spectral adjacency. To be considered for a cluster, at least three significant adjacent sensors were required. The corresponding cluster-level statistics were calculated by taking the sum of the t-values within each cluster. The largest cluster-level statistic was used as the observed cluster-based test statistic. The cluster-based test statistic distribution was approximated utilizing the Monte Carlo method with 1,000 random partitions. The proportion of random partitions that resulted in a larger test statistic than the observed one (the Monte Carlo significance probability) was compared to the critical α-value of 0.05 (two-sided). If the Monte Carlo significance probability was smaller than 0.05, the data in the "attend left" and "attend right" conditions were considered significantly different. Visual inspection of the significant positive and negative clusters was used to determine the frequency range (10–14 Hz) and sensors (O1, PO3, P3, P7, O2, PO4, P4, P8) for further analyses.

For the alpha power modulation and hemispheric lateralization analyses, the two age groups were compared using a Repeated Measures (RM) ANOVA, with memory condition (low distraction, high distraction) as a within-subject factor, age group (younger adults, older adults) as a between-subjects factor, and cPMI or LAD values as the dependent variable. All further analyses focused on the stimulus window only (250–750 ms, relative to stimulus onset). Effect sizes (partial eta-squared; η_p^2) were computed for all analyses. When a GLM was significant, post hoc tests were performed using Fisher's least significant difference procedure.

TABLE 1 Mean and standard deviation of behavioral measurements presented by age group

	Younger adults	Older adults
D-prime $targets_{LD}$	0.87 (0.36)	0.66 (0.32)
D-prime $targets_{HD}$	0.87 (0.35)	0.60 (0.31)
D-prime distractors	0.13 (0.16)	0.11 (0.20)
High-confident hits $targets_{LD}$	43.93 (23.55)	40.74 (28.08)
High-confident hits $targets_{HD}$	86.17 (40.93)	77.48 (51.83)
High-confident hits distractors	23.63 (18.03)	40.04 (35.66)

3 | RESULTS

3.1 | Behavioral results

Both younger and older adults encoded pictures that were presented to the left or right hemifield. These target pictures were presented under low- or high-distraction conditions (see Figure 1). During encoding, participants performed a semantic classification task on the target items. Performance on this semantic classification did not differ across age groups (mean accuracy: 0.85 (SD = 0.07); t(55) = 0.75, p = .46). Memory for the pictures was later tested in a recognition task. With this task, we were able to see whether younger and older adults are hindered to the same extent when there is highly distracting information present during the encoding of target information. We hypothesized that older adults would present with a lower memory performance, as compared to the younger adults. In addition, we anticipated a drop in memory performance for $targets_{HD}$, as compared to $targets_{LD}$. Furthermore, we expected this drop to be greater for older adults than for younger adults, since they would be less able to inhibit the distractors.

Behavioral results from the younger and older adults are summarized in Table 1. There was a significant main effect of age (young, old; $F(1,55) = 8.25$, $p = .006$, $\eta p^2 = 0.13$) and no significant main effect of memory condition ($targets_{LD}$, $targets_{HD}$; $F(1,55) = 1.94$, $p = .17$, $\eta p^2 = 0.034$). In addition, there was no significant interaction between age group (young, old) and memory condition ($targets_{LD}$, $targets_{HD}$) on d-prime scores ($F(1,55) = 0.31$, $p = .31$, $\eta p^2 = 0.019$). An additional t test was used to test whether there was a difference in memory for distractors, in other words, whether both age groups had comparable memory for items that were to be inhibited. This test showed no group effect on unintentional memory for distractors (t(55) = 0.55, p = .59). When we tested whether there was an age effect on the difference between target (high- and low-distraction conditions combined) and distractor d-prime, there was a significant interaction between age group (young, old) and memory condition

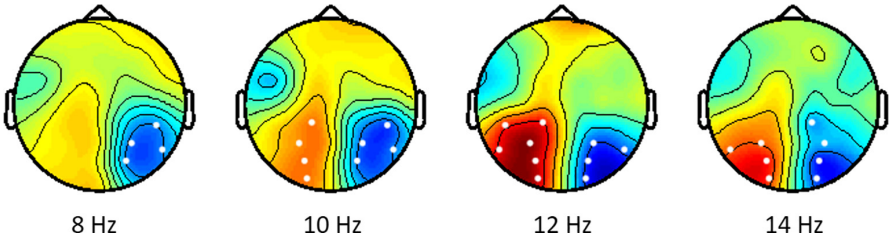

FIGURE 2 The difference between "attend left" and "attend right" TFRs (the power modulation index) with significant positive and negative clusters marked by white dots. Based on this we selected the sensors O1, PO3, P3, P7, O2, PO4, P4, P8 for further analyses

(target, distractor) ($F(1,55) = 6.25$, $p = .015$, $\eta p^2 = 0.10$). These results indicate that younger adults had a better memory for target items than the older adults, and neither younger nor older participants were impaired on target memory by distractors. Both age groups showed comparable memory performance for items that had to be inhibited during encoding. These results are not fully in line with the proposed IDT (Kane et al., 1994), since the observed lower memory performance in older adults was not modulated by the level of distraction present. However, the age-related memory decline seems to only be present for the target items, while there is no age difference in the distractor memory performance. It is a possibility that the absence of an age-related memory decline for the distractors, is due to the fact that the older adults encoded more distractors. This would suggest that older adults had more trouble inhibiting the encoding of high distractors.

Since there was no effect of the presence of distractors on memory for targets in both younger and older adults, we then asked whether the presence of distractors had an effect on memory confidence regarding targets. Memory confidence can be seen as a more sensitive measure, as compared to objective memory performance, and therefore might pick up on more subtle effects. Trial counts in the three confidence levels on target hit trials were analyzed to investigate effects on memory confidence. Results showed that there was no main effect of age group ($F(1,55) = 1.29$, $p = .26$, $\eta p^2 = 0.023$). In addition, there were no significant interactions between age group (younger, older) and memory condition ($target\text{-}s_{LD}$, $targets_{HD}$) ($F(1,55) = 2.03$, $p = .16$, $\eta p^2 = 0.036$), age group and confidence level (high, mid, low) ($F(1,55) = 0.18$, $p = .83$, $\eta p^2 = 0.003$), and age group, memory condition and confidence level ($F(2,110) = 0.68$, $p = .51$, $\eta p^2 = 0.012$) on trial counts. An additional RM ANOVA showed an interaction between age group (younger, older) and distractor hit confidence (high, mid, low) ($F(1,55) = 4.49$, $p = .013$, $\eta p^2 = 0.075$). Post hoc comparisons showed that older adults had more high-confident distractor hits, as compared to younger adults ($t(55) = 2.22$, $p = .030$). The age difference between mid-confident ($t(,55) = 0.51$, $p = .61$) and low-confident ($t(55) = 1.60$, $p = .12$) distractor hits did not reach significance. When we tested whether there was an age effect on the difference between the amount of high-confident target hits (high- and low-distraction conditions combined) and distractor responses, there was a significant interaction between age group (young, old) and memory condition (target, distractor) ($F(1,55) = 14.43$, $p < .001$, $\eta p^2 = 0.21$). In sum, this indicates that there was no difference in subjectively perceived memory confidence between younger and older adults when we looked at target items. Nevertheless, older adults were more confident when making memory decisions about distractors. These results concur with the previous results regarding objective memory: Older adults do not appear to be less able to remember target information when faced with distraction, but they do seem impaired in the inhibition of distracting information.

3.2 | EEG results

3.2.1 | Sensor selection

We first aimed to identify the sensors in which the alpha power was modulated strongly in the cue-target interval. We did this by calculating the difference between the alpha power for attending left and attend right trials and applying a cluster-based permutation test (see Methods); see Figure 2. The cluster-based permutation test revealed two clusters that differed significantly between the "attend left" and "attend right" conditions. A significant positive cluster was found over the left posterior hemisphere ($p = .005$), and a significant negative cluster was found over the right posterior hemisphere ($p = .003$; see Figure 2). Based on inspection of these clusters, further analyses in the manuscript were restricted to the 10–14 Hz range, and the following sensors: O1, PO3, P3, P7, O2, PO4, P4, P8. This choice was based upon the symmetrical significance in both clusters.

3.2.2 | Alpha modulation and lateralization

After frequencies (10–14 Hz) and sensors (O1, PO3, P3, P7, O2, PO4, P4, P8) of interest were determined, we computed the average TFRs corresponding to the selected electrodes. The power modulation index (PMI) per hemisphere was

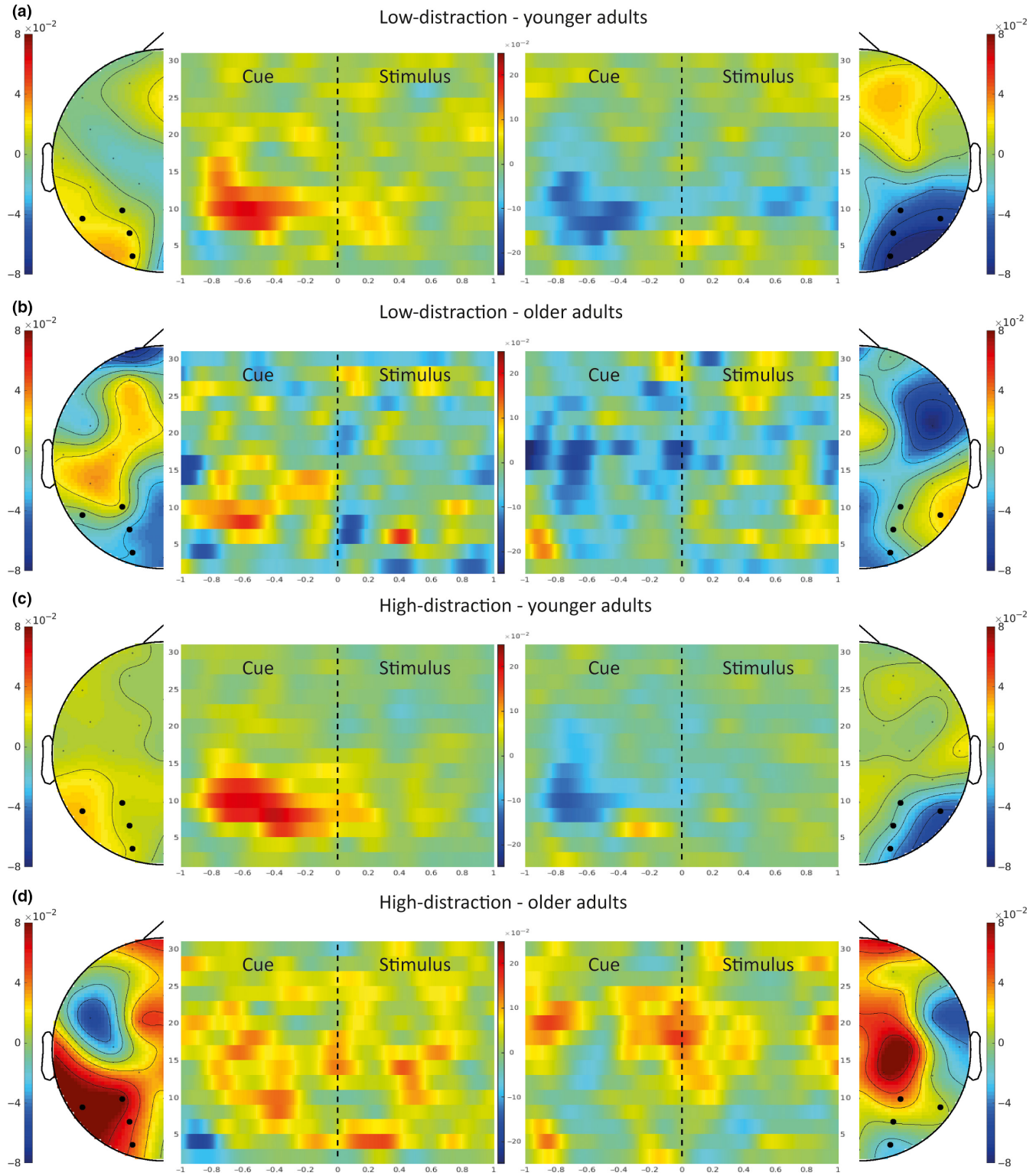

FIGURE 3 TFRs and Topographical plots (stimulation window) of the PMI belonging to the positive (left) and negative (right) electrode cluster in (a) younger adults during low distraction, (b) older adults during low distraction, (c) younger adults during high distraction, (d) older adults during high distraction. The topographical plots represent the average PMI in the stimulus window only

computed from the grand average TFRs and is presented in Figure 3. Given the PMI formula and assuming larger alpha power ipsilateral to the target location, positive PMI values are expected in the left hemisphere and negative values in the right hemisphere. A combined PMI (cPMI) measure was calculated by subtracting the average PMI of the right

hemisphere from the average PMI of the left hemisphere. Positive cPMI values indicated effective alpha modulation in the hypothesized direction. That is, higher alpha power during ipsilateral target presentation and lower alpha power during contralateral target presentation.

The next step was to see whether alpha power modulation during encoding is of functional importance during the memory task, irrespective of distraction load. If the success of encoding is related to alpha power modulation, we would expect a relation between alpha power modulation during encoding and later memory performance for all of our subjects, regardless of age group or distraction condition. To test this hypothesis, alpha power modulation, quantified as the average cPMI values during the stimulus window, was correlated with the average target d-prime. This analysis showed that the average cPMI values significantly correlated with the average target d-prime ($r_s(57) = 0.32$, $p = .016$; see Figure 4). This indicates that greater alpha modulation was associated with higher memory performance.

When we looked at the stimulus window in the low-distraction condition in Figure 3, there appears to be less power modulation in the older adults, as compared to the younger adults. Whereas in the high-distraction condition, younger adults seem to show less alpha power modulation, as compared to the older adults. CPMI values, averaged per age group and memory condition, are shown in Figure 5. The data show higher cPMI value for the younger adults in the low-distraction condition, while cPMI values in the high-distraction condition appear similar across age groups.

These observations were tested by conducting a RM ANOVA, which revealed no significant main effect of memory condition ($F(1,55) = 1.035$, $p = .31$, $\eta p^2 = 0.018$) and age group ($F(1,55) = 3.05$, $p = .087$, $\eta p^2 = 0.052$). There was a significant interaction effect between memory condition (low distraction, high distraction) and age group (young, old) ($F(1,55) = 5.23$, $p = .026$, $\eta p^2 = 0.087$). Post hoc t tests showed that there was no significant difference between the low- and high-distraction condition in the younger adults ($t(29) = 1.07$, $p = .30$) and for the older adults the difference approached significance ($t(26) = -2.01$, $p = .055$). In addition, there was a significant difference between age groups in the low-distraction condition ($t(55) = 2.54$, $p = .014$), and it was confirmed that there was no significant difference in the high-distraction condition ($t(55) = 0.10$, $p = .92$). When cue-related cPMI values were added as a covariate to the stimulus-related analyses, the pattern of results was similar. This indicates that during low distraction, the older adults show less alpha modulation in the hypothesized direction, as compared to younger adults. This suggests a difference in inhibitory mechanisms between older and younger adults when little distraction is present.

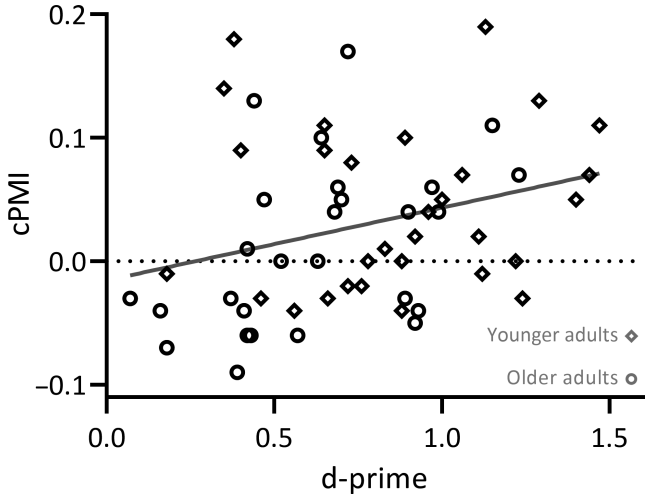

FIGURE 4 Relationship between mean cPMI values and mean target d-prime values over high- and low-distraction conditions

Next, we focused on the effect of memory condition on ipsi- and contralateral alpha power, relative to the target. We expected that, in order to successfully suppress the distractor, there would be more alpha power ipsilateral to the target during high-distraction, as compared to the low-distraction condition. In addition, we expected that, in order to successfully process the target, there would be less alpha power contralateral to the target during high-distraction, as compared to the low-distraction condition. To compare lateralized alpha power during low and high distraction, we computed LAD_{ipsi} and LAD_{contra}, where positive LAD_{ipsi} values represent an increase in ipsilateral alpha power from the low- to the high-distraction condition, and negative LAD_{contra} values represent a decrease in contralateral alpha power from the low- to the high-distraction condition.

The LAD_{ipsi} and LAD_{contra} values during the stimulus window, are shown in Figure 6, averaged per age group and memory condition. This figure shows that for the younger adults there is lower ipsilateral and higher contralateral alpha power during high distraction, as compared to low distraction. This pattern is opposite for the older adults, who show higher ipsilateral and lower contralateral alpha power during high distraction, as compared to low distraction. This observation was tested by conducting a RM ANOVA, which revealed no significant main effect of laterality ($F(1,55) = 0.35$, $p = .56$, $\eta p^2 = 0.006$) and age group ($F(1,55) = 0.20$, $p = .66$, $\eta p^2 = 0.004$). There was a significant interaction effect between laterality (ipsilateral, contralateral) and age group (young, old) ($F(1,55) = 4.05$, $p = .049$, $\eta p^2 = 0.069$). However, post hoc t tests showed no significant difference between age groups on LAD_{ipsi} ($t(55) = 1.32$, $p = .19$) and LAD_{contra} ($t(55) = 0.72$, $p = .48$), and no difference between LAD_{ipsi} and LAD_{contra} for both younger ($t(29) = -1.14$, $p = .27$) and older adults ($t(26) = 1.64$, $p = .11$). These results indicate that younger and older adults show the opposite pattern in the effect of memory condition on ipsi- and contralateral alpha power. Where older adults show a pattern that

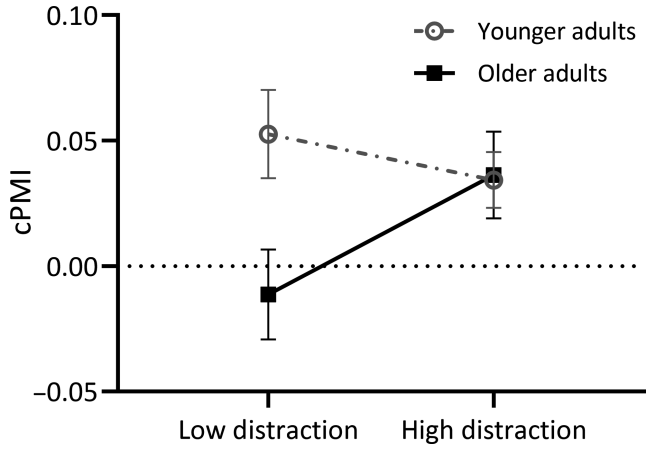

FIGURE 5 The cPMI during stimulus presentation in the alpha band (10–14 Hz), for younger and older adults, per memory condition. CPMI represents the combined power modulation index. There was a significant difference between the cPMI for older and younger adults in the low-distraction condition. This suggests that during low levels of distraction younger and older adults employ different inhibitory mechanisms. Error bars represent standard errors

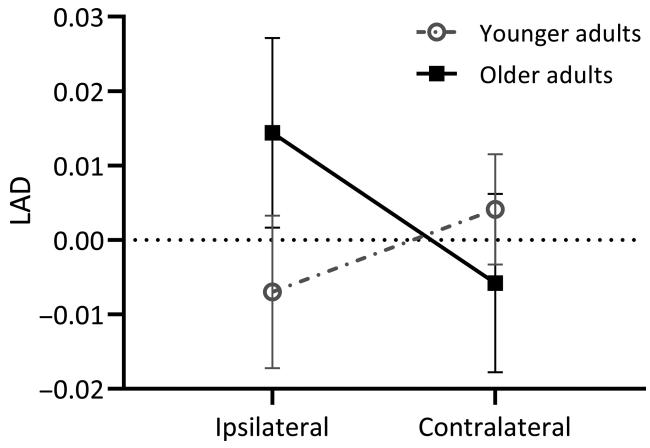

FIGURE 6 The LAD during stimulus presentation in the alpha band (10–14 Hz), for younger and older adults, per memory condition. LAD represents the mean alpha power difference between low- and high-distraction conditions in the ipsilateral and contralateral hemisphere

is consistent with our prediction, of increased ipsilateral and decreased contralateral alpha power during high distraction.

4 | DISCUSSION

The aim of the present study was to explore whether alpha power modulation is involved in memory encoding under distracting conditions and if this holds true for both younger and older adults. Laterally presented target words were either encoded in a low- or high-distraction condition. This lateralized encoding task enabled us to compare alpha modulations in both age groups and relate this to memory performance. Given that it has been previously reported that older adults have inhibitory difficulties (Devitt et al., 2016; Kane et al., 1994; Mund et al., 2012; Zanto et al., 2010) and show aberrant alpha modulations (Hong et al., 2015; Leenders et al., 2018; Rogers et al., 2018), we compared memory performance and alpha power modulation between age groups. Since we expected that alpha power modulation would be of greater importance when distraction is high, we considered the difference in alpha power modulation between low- and high-distraction conditions. Our results showed that older adults remembered fewer target items, but had similar memory and higher confidence for distractors, compared to younger adults. Additionally, we confirmed that the degree of alpha power modulation shows a positive relationship with memory performance. Last, we saw that—in contrast to our expectation—older adults only modulated alpha power during the high-distraction condition. We will now discuss the possible implications of these findings.

4.1 | Older adults had reduced target memory performance, while confidently remembering distractors

The behavioral results show that, compared to younger adults, older adults had a lower memory performance for targets, indicative of age-related memory decline (Small, 2001; Wang et al., 2011). We hypothesized that target memory would be lower in the high-distraction condition than in the low-distraction condition and that following the IDT, this effect would be most pronounced for the older adults (Hasher et al., 1988; Kane et al., 1994; Lustig et al., 2007). In contrast to our hypothesis, we observed that in both age groups target memory and confidence seemed unaffected by the level of distraction present in the opposite hemifield. However, it was not the case that the distractors were completely ignored by our participants. Distractors were unintentionally remembered, and thirty-seven percent of these hits were made with high confidence. It is interesting that distractor memory showed no age-related memory decline and older adults even expressed more distractor memory confidence. This implies that older adults are still impaired in the inhibition of distracting information that captures bottom-up attention. Our behavioral results thus suggest that older adults have trouble inhibiting highly distracting information without impairment in memory for targets, which has been reported before (Biss et al., 2013; Lustig & Jantz, 2015; Thomas & Hasher, 2012). Older adults thus seem to be able to use top-down control to compensate for their higher distractibility.

4.2 | Alpha power modulation predicts successful memory encoding across subjects

Top-down inhibitory control might be one of the mechanisms responsible for the compensation of distraction during memory encoding (Lenartowicz et al., 2016). Inhibitory control is thought to be supported by a frontoparietal attentional network, that modulates sensory neuron excitability through alpha power (Corbetta & Shulman, 2002; Uncapher & Wagner, 2009; Wang et al., 2016). Additionally, alpha power modulation during encoding has been shown to be beneficial for memory performance. (Jiang et al., 2015; Park et al., 2014). Our current results concur with this finding and show a positive relationship between the amount of alpha power modulation during encoding and subsequent memory performance. Therefore, we can infer that top-down inhibitory control, as measured by alpha power modulation, promotes the encoding of information under distracting conditions. Now that we have confirmed this positive relationship in the current study, the next step was to investigate whether older adults are utilizing alpha power modulation to compensate for higher distractibility.

4.3 | Older adults utilize alpha power modulation, but only during high distraction

When we consider Figure 5, we see that younger adults show comparable levels of alpha modulation in both conditions, while older adults seem to only modulate alpha power in the high-distraction condition. This suggests that younger adults were actively trying to focus their attention on the targets, leading to better memory performance. It is unclear why older adults did not appear to show alpha power modulation in the low-distraction condition. However, it might explain why older adults had a lower memory performance for $targets_{LD}$, as compared to younger adults. Maybe their failure to recruit compensatory top-down inhibitory mechanisms (Sander, Lindenberger, et al., 2012) is partly responsible for their lower memory performance when there is little distraction present. During high distraction, compensatory top-down attentional control might not be enough to equal memory performance between age groups, but might help them to not decline further. This could indicate that older and younger adults are both utilizing similar mechanisms to distribute attentional resources when faced with distraction. However, in older adults the threshold for alpha modulation might be higher, leading to little alpha modulation during low distraction.

4.4 | Inhibition deficits in older adults might be task-dependent

It has been suggested before that older adults do not use alpha power modulation to inhibit irrelevant information (Hong et al., 2015; Vaden et al., 2012), here we argue that older adults are able to use alpha power modulation, but only when the distraction is large enough. Previous studies with relatively low distraction conditions have reported that older adults do not show alpha modulation (Deiber et al., 2010; Hong et al., 2015; Sander et al., 2012; Vaden et al., 2012). For instance, when cued to ignore a stimulus in isolation, younger adults showed alpha suppression, while older adults showed a trend in the opposite direction (Vaden et al., 2012). When we consider the low-distraction condition in Figure 3b and Figure 5, we also see this trend toward alpha modulation in the non-optimal direction, in favor of distractor processing. On the other hand, when the level of distraction is higher, older adults are able to modulate alpha activity to optimize target processing and diminish distractor processing (Leenders et al., 2018; Mok et al., 2016). Our results from the high-distraction condition are in agreement with this finding. More generally, as predicted by the IDT, older adults show higher distractibility and sustained access to non-target information. However, they are able to recruit top-down attentional control mechanisms and maintain performance levels when attentional demands are higher. The age-related memory effect we observed during low distraction is possibly due to inefficient top-down control when attentional demands are low. Therefore, our results are not fully in support of the IDT, but can also not rule out that there is an interaction with the level of distraction present (Sander, Werkle-Bergner, et al., 2012) or timing of neural responses (Deiber et al., 2010; Gazzaley et al., 2008). Perhaps, future memory studies with more distraction levels are able to shed more light on this.

4.5 | Limitations

Unfortunately, due to the limited number of trials, especially in older adults, we were not able to perform subsequent memory analyses on the oscillatory data. This was mainly because of trial rejection due to saccades. However, we did confirm the functional relevance of alpha power modulation in memory encoding. We hope that the results we present here will be followed-up by future studies able to perform trial-based analyses. These future studies might benefit from an additional session to thoroughly train their participants not to make saccades toward the stimuli.

In addition, our method of saccade rejection was based upon individualized thresholds. This means that trials in which the participant looked directly at the stimuli were removed. We believe that this method is more sensitive to picking up saccades than other methods (e.g., visual inspection or ICA) since it is based upon the participants' individual threshold determined during the experimental session. However, we realize that smaller saccades, where the focus

was not on the stimulus, are not removed with this threshold. But since covert attention is still needed to identify the target, we believe alpha power will still show lateralization in this case. Indeed, additional analyses on the horizontal EOG data after saccade removal (not reported here) did not yield results indicating that our findings were explained by saccade artifacts.

5 | CONCLUSIONS

Here we demonstrate that alpha power modulation during encoding, related to top-down inhibitory control, is predictive of later memory performance and is used by both younger and older adults. However, older adults only used alpha power modulation as an inhibitory mechanism during high distraction. We believe that the alpha power modulation enabled the younger and older adults to maintain target memory performance levels when faced with distracting information. Therefore, even though older adults show signs of higher distractibility, their top-down inhibitory control can preserve long-term memory performance.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ejn.15086.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author.

ORCID

Syanah C. Wynn https://orcid.org/0000-0002-8002-9772

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