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Older adults, unlike younger adults, do not modulate alpha power to suppress irrelevant information

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Abstract

This study examines the neural mechanisms through which younger and older adults ignore irrelevant information, a process that is necessary to effectively encode new memories. Some age-related memory deficits have been linked to a diminished ability to dynamically gate sensory input, resulting in problems inhibiting the processing of distracting stimuli. Whereas oscillatory power in the alpha band (8–12Hz) over visual cortical areas is thought to dynamically gate sensory input in younger adults, it is not known whether older adults use the same mechanism to gate out sensory input. Here we identified a task in which both older and younger adults could suppress the processing of irrelevant sensory stimuli, allowing us to use electroencephalography (EEG) to explore the neural activity associated with suppression of visual processing. As expected, we found that the younger adults' suppression of visual processing was correlated with robust modulation of alpha oscillatory power. However, older adults did not modulate alpha power to suppress processing of visual information. These results demonstrate that suppression of alpha power is not necessary to inhibit the processing of distracting stimuli in older adults, suggesting the existence of alternative strategies for suppressing irrelevant, potentially distracting information.

Keywords

Aging; Attention; EEG; Oscillations; Sensory gating; Visual working memory

1. Introduction

Effective encoding of memories requires that we attend to relevant stimuli and also that we ignore irrelevant or competing stimuli. Some memory encoding deficits for older adults (OA) have been connected to a decline in their ability to ignore irrelevant, potentially distracting stimuli (Hasher and Zacks, 1988; Dempster, 1992; May et al., 1999; Gazzaley et al., 2005).

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Conflict of interest:

The authors have no conflicts of interest regarding these data and all data were acquired according to NIH and UAB ethics standards

Previous research has investigated the mechanisms through which healthy young adults (YA) are able to ignore irrelevant stimuli (for example, Vogel et al., 2005; Giesbrecht et al., 2006; Weissman et al., 2006; Händel et al., 2010). One hypothesis is that, in younger adults, oscillatory activity in visual cortical areas dynamically gates sensory input (Kelly et al., 2006; Thut et al., 2006; Jensen and Mazaheri, 2010; Foxe and Snyder, 2011; Hanslmayr et al., 2011). This hypothesis holds that when ongoing alpha band power is strong, participants successfully inhibit processing of irrelevant stimuli in working memory tasks (Klimesch, 1999).

These two lines of evidence -- 1) older adults' memory problems may derive from inability to ignore distracting information, and 2) younger adults show strong alpha power before a to-be-ignored stimulus -- led us to hypothesize that older adults' deficits in ignoring irrelevant information stem from the inability to modulate alpha power. In the present study, we identified a task in which both younger and older adults show behavioral evidence of suppression of distracting information, and compared the EEG correlates of suppression in both groups. This enabled comparisons of the neural mechanisms of successful suppression in younger and older adults, and indicates that older adults do not modulate alpha power to gate sensory input.

Processing new visual information interferes with visual information held in working memory (Yotsumoto and Sekuler, 2006). One behavioral measure of suppression of irrelevant information is the degree to which the to-be-ignored stimulus interferes with memory of the to-be-remembered stimulus (Yotsumoto and Sekuler, 2006; Huang and Sekuler, 2010). The experiment described here examines EEG activity during preparation for stimuli that are to-be-ignored and to-be-remembered. We also compare sets of trials on which a to-be-ignored stimulus was "more successfully" vs. "less successfully" ignored.

2. Material and methods

2.1 Participants

Twenty-six participants were recruited from the University of Alabama at Birmingham community: 15 younger adults (mean age=26, range=19–35, 9 male) and 11 older adults (mean age=69, range=62–79, 6 male). Working memory was assessed via digit span, backward digit span, and letter-number sequencing subsections of the Wechsler Adult Intelligence Scale in all participants. In addition, 10 of 11 older adults had performed an extensive neuropsychology battery verifying that they did not have mild cognitive impairment. The remaining older adult reported no signs of dementia and showed normal working memory scores. All participants had normal or corrected-to-normal visual acuity, verified with a Snellen eye chart.

2.2 Task

Participants performed three change detection tasks (Vogel and Machizawa, 2004) in randomized, counterbalanced blocks of 60 trials each, for a total of 240 trials per condition (Figure 1). In the *Remember1* condition, participants viewed a display (S1) of oriented bars (2 bars on each side of a fixation cross), and judged whether a subsequently presented probe (P1) differed from that display (S1). In the *Remember2* condition, participants viewed two sequentially presented stimulus arrays (S1 and S2) followed by two probes (P1 and P2). The *Ignore* condition is similar, but participants were not tested on S2 and instead were instructed to ignore it. Participants pushed the “same” button if the stimulus and probe matched and the “different” button if they differed. Feedback tones of 1000Hz and 500Hz were played following correct and incorrect responses respectively. If the participant did not respond, two incorrect tones were played. All auditory stimuli were transmitted through E-A-RTone Gold 3A Insert Earphones from Etymotic Research (Elk Grove Village, IL).

2.3 Stimuli

Stimuli were presented using Psychophysics Toolbox (Brainard, 1997) within MATLAB (MathWorks, Natick, MA) on an Apple Mac Mini running OSX 10.5.8 with a CRT monitor ($36\times26.5cm^2$ visual area, resolution 1024×768 pixels, refresh rate 85Hz). The stimuli were blue rectangular bars each measuring 0.3 by 0.7 degrees visual angle and appeared in random positions within a visual area of 3.7 by 2.5 degrees on each side of the fixation cross. Stimuli could be as close as 1.02 degrees horizontally from fixation. The bars were oriented at a randomly chosen angle (0, 45, 90, or 135 degrees) from the vertical. The background was gray and the cue arrow and fixation cross were black. When the probe array differed from the stimulus, only one of the oriented bars was changed: its orientation was shifted by 90 degrees. An example is shown in the top row of Figure 1.

2.4 Data Acquisition

Data were collected over two sessions on two separate days, with the number of trials of each condition the same on each day. Participants first read the task instructions on their own and then received redundant instruction verbally. When participants reported full understanding of the task, two practice sessions of 12 trials for each condition were administered. The first practice session presented the task instructions on the screen along with the stimuli. The presentation time intervals were exaggerated to allow time to read the instructions and practice the task. The second practice session was a short version of the actual task.

Participants were seated in a sound attenuated booth with head stabilized by a chin rest 93cm from the stimulus display. EEG data were acquired using a NeuroScan 64 channel Quick-Cap with MagLinkRT software sampling at 1000Hz. Eye tracking was used to verify that all participants fixated on the cross and not the stimuli (SR Research), and that there were no systematic saccades during or before presentation of S2. A light sensing diode verified the timing of stimulus onset.

2.5 Data and Statistical Analysis

Preprocessing of the EEG data was done using EEGLab Toolbox (Delorme and Makeig, 2004) within MATLAB. Correct and incorrect trials were separated for each condition (*Remember1*, *Remember2*, and *Ignore*). Trials were then epoched around S2 onset with a window of 2 seconds (−1 second to +1 second). All trials containing eye blinks, eye electrode activity consistent with saccades, or muscle artifact were discarded based on visual inspection (number of correct trials after artifact rejection: younger adults mean: R1=157, IG=163, R2=108; older adults mean: R1=111, IG=117, R2=54). The data were analyzed using the Fieldtrip Toolbox (Oostenveld et al., 2011) within MATLAB using Hanning tapers. Data were band pass filtered between the frequencies 2–20Hz. Because the tasks required visual attention, electrodes of interest were parietal electrodes (P1, P2, P3 and P4) over which visually-evoked activity depends on visual attention (Hillyard and Anllo-Vento, 1998). These electrodes were chosen rather than occipital electrodes because stronger visually-evoked event-related potentials (ERPs) are observed in these electrodes, and occipital electrodes may be more susceptible to muscle artifact. Because raw alpha power differs between younger and older adults (Klimesch, 1999), analysis of the power in the alpha band was performed both defining the peak alpha frequency on a participant-by-participant basis, as well as defining alpha power identically for each participant. To define the peak alpha frequency for each participant, the frequency between 8–12Hz with the maximum power value in the 400 ms window before S2 during the *Ignore* condition was calculated. The mean of this value for each of the four electrodes of interest for each participant was used as his or her individual alpha peak. All analyses of the difference between *Ignore* and *Remember2* trials were normalized using the formula (*Ignore* – *Remember2*) / (*Ignore* + *Remember2*) for each participant in order to decrease any effects due to across-participant variability in alpha power.

3. Results

3.1 WAIS Analysis

Working memory was assessed via digit span, backward digit span, and letter-number sequencing subsections of the Wechsler Adult Intelligence Scale in all participants. No significant difference was found between age groups for backward digit span or letter-number sequencing. However, older adults performed significantly better on the digit span task than younger adults (p=0.042 older adult mean = 11.18, younger adult mean = 9.53), further evidence that this was a group of high-functioning older adults.

Participants performed a set of three visual short-term memory tasks requiring them to either ignore or remember a stimulus (Figure 1). Tasks were blocked so that participants knew which task was to be performed on any trial. EEG measures of ongoing alpha oscillations and event related potentials were recorded, and the resulting data were compared between groups.

3.2 Behavioral Evidence of Suppression

Although older adults had slower reaction times and made more errors (Figure 2), both groups performed well when asked to remember only one stimulus (*Remember1*). An ANOVA on reaction times with factors of group (younger vs. older adults) X task (*Remember1*, *Remember2*, and *Ignore*), showed a significant main effect of group (p=0.0034), an effect of task (p<0.0001), and no interaction (p=0.55). An ANOVA on proportion error, with factors of group X task, showed main effects of both group and task (p<0.0001), and an interaction (p=0.021). Remembering two stimuli (*Remember2*) was more difficult than *Remember1* for both younger and older adults, resulting in more errors (t-test p<0.001) and slower reaction times (younger adults t-test p=0.050, older adults t-test p=0.0011). However, when instructed to ignore the second stimulus (*Ignore*), performance improved dramatically. Reaction times on the *Ignore* condition were statistically indistinguishable from *Remember1* for both younger adults (p=0.87) and older adults (p=0.96). Proportion error was not different between *Remember1* and *Ignore* conditions for older adults (p=0.16). Interestingly, younger adults made significantly more errors in the *Ignore* condition than in *Remember1* task (p=0.030). This evidence shows that older adults were able to suppress irrelevant information just as well as, if not better than, younger adults in this task.

The *Remember2* task was the only one that required two responses. Responses to the second probe of *Remember2* were more accurate for younger adults than for the older adults (younger: mean percent correct 73; older: mean percent correct 56; t-test p=0.0014).

3.3 ERP Evidence of Suppression in Older Adults

As described in Methods, our task required that participants determine whether or not a to-be-remembered image had been altered upon subsequent presentation. A cue at the beginning of each trial indicated whether the change would occur on the left or right side of the image. However, we did not find significant differences in event-related potentials (ERPs) between the contralateral and ipsilateral hemispheres. Similarly, no significant hemispheric differences were observed in prestimulus alpha oscillations for younger or older adults. This is unsurprising, as the stimuli were not highly lateralized; they could be as close as 1.02 degrees from central fixation. Therefore, laterality effects will not be described further.

ERPs were analyzed as a measure of the degree of stimulus processing. Previous work (Hillyard and Anllo-Vento, 1998) indicates that the first positive (P1) and negative (N1) going peaks are sensitive to attention. The difference between the P1 and N1 peak amplitudes of the ERPs from the *Remember2* and *Ignore* conditions was used as a measure of attentional modulation (Rugg et al., 1987; Hillyard and Anllo-Vento, 1998; Luck et al., 2000). As expected, we observed larger ERP amplitudes for attended (*Remember2)* than for ignored (*Ignore)* stimuli (Figure 3A). Individual participant bar graphs showing differences calculated based on the P1 and N1 peaks is shown in Figure 3B. This difference is significant for both younger (p=0.035) and older adults (p=0.032), corroborating behavioral performance with EEG evidence that older adults are suppressing irrelevant information. Further, the interaction between younger and older adults ERP modulation was not significant (p=0.17), indicating that for this task, older and younger adults do not suppress the processing of irrelevant information differently. The N1 latency was calculated for both younger adults (Remember2=173.30ms and Ignore=175.47ms) and older adults (Remember2=177.73ms and Ignore=190.82ms). An ANOVA on N1 latency with factors of group X task, showed no significant main effect of group (p=0.22) nor effect of task (p=0.075), and no interaction (p=0.15).

3.4 Alpha Modulation in Younger and Older Adults

ERP and behavioral results indicate that, for this task, older adults are able to more extensively process the to-be-remembered stimulus than the to-be-ignored stimulus (Figures 2 & 3). Several studies have suggested that strong alpha band power prior to stimulus presentation reflects preparation to ignore the upcoming stimulus (Kelly et al., 2006; Thut et al., 2006; van Dijk et al., 2008; Snyder and Foxe, 2010). This hypothesis predicts that modulation of attention in both younger and older adults will be accompanied by modulation of prestimulus alpha power. However, during the 400ms period prior to S2, only younger adults modulate alpha power (ANOVA, interaction of group by task p=0.017). Younger adults showed more alpha power when instructed to ignore than to remember (t-test p=0.039), consistent with the hypothesis that alpha is used to suppress processing of visual information (Figure 4C). Older adults, on the other hand, show a trend in the opposite direction (Figure 4B). These data indicate that the role of alpha modulation in suppression of irrelevant information differs between younger and older adults. The data shown are for the parietal electrodes that were chosen a priori based on previous work indicating they would likely show strong effects of visual attention (Hillyard and Anllo-Vento, 1998). However, the direction of these results was the same regardless of whether parietal, occipital, or frontal electrodes were used. This indicates that there is not simply a shift in topography of activity with age.

Older adults show alpha band peaks at slower frequencies (Klimesch, 1999, Figure 4A). Older adults' peak frequencies were, on average 9.8 Hz, while the mean for younger adults was 10.8 Hz (t-test p=0.012). Additionally, we found that older adults showed weaker alpha power than younger adults (t-test p=0.017). To prevent a bias due to individual participants' different peak alpha frequencies, all analyses of alpha modulation presented above were performed on the individual participants’ alpha band peak.

To control for the possibility that these effects depend on the selection of individuals' peak alpha frequencies, these analyses were also performed defining the alpha band power as the band from 10–12Hz for all participants. The effect was the same: younger adults showed significant modulation (paired t-test p=0.045) between conditions with more alpha power when instructed to ignore than remember and the difference in modulation between younger and older adults was significant (t-test p=0.016).

3.5 Alpha During Correct and Incorrect Ignore Trials

Younger adults' modulation of prestimulus alpha power between *Ignore* and *Remember2* conditions supports the hypothesis that alpha is used to suppress incoming information, but does not directly relate alpha power to performance. In order to test the relationship between alpha power and performance, prestimulus alpha before S2 for correct and incorrect *Ignore* trials were compared. If alpha is associated with suppression of irrelevant information, we expect high alpha power during correct trials and low alpha power during incorrect trials. For younger adults, this relationship was true: prestimulus alpha power between correct and incorrect trials is significantly different for younger adults (paired t-test p=0.0035). The relationship did not hold for older adults, however (p > 0.05). The difference between younger and older adults was significant (t-test p=0.030). Successful suppression of irrelevant information is correlated with greater prestimulus alpha power for younger adults, but not for older adults.

4. Discussion

4.1 Both younger and older adults suppress irrelevant information

As expected, older adults made more errors and had slower reaction times on the behavioral task than did younger adults. However, both age groups performed significantly better in the *Ignore* than *Remember2* condition. This indicates that, although overall task performance was better in younger adults, older adults were able to ignore distracting information at least as well as their younger counterparts.

Consistent with behavioral performance, ERP amplitudes were smaller for ignored stimuli and larger for remembered stimuli. Given previous work showing that ERP amplitudes vary with suppression of irrelevant information and attention (for example, Rugg et al., 1987; Hillyard and Anllo-Vento, 1998; Luck et al., 2000), this provides neural evidence that both younger and older adults suppressed irrelevant information in the *Ignore* condition.

Together, the behavioral and ERP evidence indicate that, for this paradigm, older adults suppress distracting information to a degree that is at least equivalent to their younger counterparts (Figures 2 & 3). Previous studies have shown that older adults' ability to ignore irrelevant information is impaired in some contexts, (Hasher and Zacks, 1988; Lavie and Fox, 2000; Gazzaley et al., 2005). In the task used here, however, both younger adults and older adults successfully ignored irrelevant information. This is likely because the task demands are different from those in other studies. This paradigm may be easier for older adults to suppress distracting information, perhaps because this paradigm uses relatively un-crowded visual displays and participants knew when distracting stimuli would be presented. Because older adults were able to suppress distracting information in our paradigm, we were able to compare the contribution of anticipatory alpha power to successful supression of irrelevant information in younger and older adults.

4.2 Anticipatory alpha power in younger adults

A great deal of recent research has focused on the idea that ongoing oscillations in the alpha band prior to a to-be-ignored stimulus may reflect suppression of stimulus-driven information processing (Kelly et al., 2006; Thut et al., 2006; Jensen and Mazaheri, 2010; Foxe and Snyder, 2011; Gould et al., 2011; Hanslmayr et al., 2011; Rohenkohl and Nobre, 2011). For example, Thut and colleagues (2006) showed that higher levels of ongoing alpha power before a near-threshold stimulus made it less likely to be observed. These anticipatory changes in alpha power prior to stimulus presentation may be a marker of a participant's task state, where weak alpha power indicates preparation to fully process incoming visual stimuli and higher alpha power indicates preparation to suppress processing of incoming visual stimuli (Ray and Cole, 1985; Sauseng et al., 2007, 2009; Mathewson et al., 2009; Jensen and Mazaheri, 2010).

It should be noted that several studies suggest that the behavioral effect of anticipatory ongoing alpha oscillations follows an inverted u-shaped curve, where both very high and very low values are detrimental to performance (Linkenkaer-Hansen et al., 2004; Rajagovindan and Ding, 2011). Additionally, anticipatory alpha oscillations in different parts of cortex may serve different functions (Mo et al., 2011). Given that most experiments use correlative methods, it is also possible that the changes in alpha power with attention are correlated with, but do not directly impact, performance (but see Romei et al., 2010). However, the consensus appears to be that for younger, healthy adults, modulations in alpha power over occipital and parietal cortex are a marker of the anticipatory state of the participant (Thut et al., 2006; van Dijk et al., 2008; Romei et al., 2010). Our data support this consensus (Figure 4A), showing that younger adults, there is stronger alpha power during anticipation of a to-be-ignored stimulus.

If this interpretation is correct, and anticipatory alpha power reflects preparation for a to-be-ignored stimulus, given the fact that individuals' task state fluctuates over time, the level of preparation will also fluctuate over time. If modulations of alpha power truly reflect a gating of visual input, we would expect that on *Ignore* trials where alpha power was high, participants would be more likely to suppress the distracting information in S2. On the other hand, on *Ignore* trials where alpha power was low, this distracting information would not be suppressed, leading to more errors. Thus, for participants who use alpha power to modulate visual processing, alpha power should be, on average, higher before S2 for correct trials, and lower for incorrect trials. Consistent with this hypothesis, younger adults show a very strong modulation of alpha power between correct and incorrect trials (Figure 5). This further data strengthens the claim that, for younger adults, alpha power acts functionally to gate out irrelevant, potentially distracting information.

4.3 Hemispheric differences due to spatial attention

As previously noted, although participants were cued about which side to attend for a changing stimulus, we did not observe contralateral versus ipsilateral differences in ERPs or alpha band oscillations. Other experimental paradigms show laterality effects in EEG in which stimuli in the unattended hemifield are considered “distractors” and, therefore, electrodes contralateral to the cue yield EEG results that differ from ipsilateral electrodes (Thut et al., 2006; Sauseng et al., 2009). The absence of a strong laterality effect is not surprising in our study given that the stimuli were all relatively close to fixation. The closest stimuli on either side were 1 degree from fixation, as opposed larger minimum eccentricities in papers showing strong laterality effects: 26.5 degrees minimum eccentricity, for example in work by Thut and colleagues (Thut et al., 2006), and as close as 4 degrees eccentric in an experiment by Sander and colleagues (Sander et al., 2011), where they also blocked the cues for 30 consecutive trials to emphasize the laterality effects. Thus our paradigm, with such central stimuli, is best suited for examining the temporal effects of ignoring and not the spatial effects.

4.4 Older and younger adults may not use the same neural strategies to suppress distracting information

Our data suggest that older adults are able to suppress irrelevant information in this task, but do so using different mechanisms from younger adults. Age-related changes in anatomy or function of brain circuits may drive younger and older adults to employ different neural strategies for the same cognitive task (Paxton et al., 2007; Vallesi et al., 2010; Zanto et al., 2010; Jost et al., 2011). Zanto and colleagues showed that older adults do not tend to use timing-based cues to improve their performance on attentiondemanding tasks (Zanto et al., 2011). It may be that older adults adopt different strategies than younger adults for tasks that require modulations in attention.

That the two groups adopt different mechanisms for modulating visual input implies at least two separable mechanisms through which modulation can happen. Work examining changes in brain activity with aging has found that older adults tend to recruit occipital cortex for stimulus processing less than younger adults, but recruit regions within the prefrontal cortex more strongly than do younger adults; this has been called the Posterior Anterior Shift in Aging (PASA) hypothesis (reviewed in Dennis and Cabeza, 2008). The results described here and the PASA hypothesis both suggest that older adults use different mechanisms for controlled processing than do younger adults. Further work is needed to explore how the two ideas are related, and to further dissociate the control mechanisms used by older and younger adults.

Overall alpha power and peak frequency appear to decline with age (Figure 4 and Klimesch, 1999), perhaps rendering modulation of prestimulus alpha no longer viable as a neural mechanism for attentional gating. Older adults' deficits in suppressing irrelevant information may, therefore, arise from adopting an alternate, inferior strategy (De Sanctis et al., 2009; Vallesi et al., 2010; Guerreiro and Van Gerven, 2011; Jost et al., 2011).

Our data support this hypothesis. We find that, consistent with previous work (Kelly et al., 2006; Thut et al., 2006), suppression of irrelevant information is associated with increased prestimulus alpha power in younger adults (Figure 4B). This prestimulus increase is not seen in older adults, despite the fact that older adults clearly filter out the distracting information in this paradigm. This strongly suggests that older adults do not use alpha power to ignore distracting stimuli. Thus older and younger groups may use different methods to filter out irrelevant information. Further evidence toward this conclusion comes from the analysis of correct vs. incorrect *Ignore* trials shown in Figure 5. For younger adults, there is a strong modulation of alpha power for correct vs. incorrect trials, consistent with the idea that the level of preparatory alpha power influences performance. However, older adults show no hint of this effect (and an interaction of correctness by group was significant). These data bolster the argument that older adults are not using alpha power for suppression of irrelevant information: random fluctuations in alpha power do not impact their performance.

The data thus demonstrate that both younger and older adults suppress distracting information in this paradigm. Younger adults use alpha power to gate visual input, while older adults do not use that mechanism.

4.5 Less alpha power and less alpha power modulation in older adults

Why might alpha power modulation differ between younger and older adults? Older adults have weaker alpha power (see Figure 4A and Klimesch, 1999), limiting the range of values available. Older adults may, therefore, be physically unable to modulate their alpha power in the range that is behaviorally useful (Palva and Palva, 2007; Rajagovindan and Ding, 2011). On the other hand, if older adults can be trained to use younger adult-like strategies, such as modulation of prestimulus alpha (Kelly et al., 2006; Thut et al., 2006; Gould et al., 2011; Rohenkohl and Nobre, 2011) to suppress irrelevant information, some of their working memory problems may be ameliorated. The nature and feasibility of such training presents an exciting prospect for future work.

5. Conclusion

Behavioral and EEG evidence showed that for this task, both older and younger adults successfully ignored irrelevant information. These data, along with previous studies, support the hypothesis that younger adults use increased alpha power to suppress irrelevant, distracting information. In contrast, suppression of distracting stimuli in older adults is not associated with alpha power modulation.

These results imply that older adults employ different neural strategies to ignore irrelevant information than do younger adults.

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References

Brainard DH. The Psychophysics Toolbox. Spatial Vision. 1997; 10:433–436. [PubMed: 9176952]

Delorme A, Makeig S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. Journal of Neuroscience Methods. 2004; 134:9–21. [PubMed: 15102499]

Dempster FN. The rise and fall of the inhibitory mechanism: Toward a unified theory of cognitive development and aging. Developmental Review. 1992; 12:45–75.

Dennis NA, Cabeza R. Neuroimaging of healthy cognitive aging. canlabpsychpsuedu. 2008

van Dijk H, Schoffelen J-M, Oostenveld R, Jensen O. Prestimulus oscillatory activity in the alpha band predicts visual discrimination ability. J Neurosci. 2008; 28:1816–1823. [PubMed: 18287498]

Foxe JJ, Snyder AC. The Role of Alpha-Band Brain Oscillations as a Sensory Suppression Mechanism during Selective Attention. Frontiers in psychology. 2011; 2

Gazzaley A, Cooney JW, Rissman J, D'Esposito M. Top-down suppression deficit underlies working memory impairment in normal aging. Nature neuroscience. 2005; 8:1298–1300.

Giesbrecht B, Weissman DH, Woldorff MG, Mangun GR. Pre-target activity in visual cortex predicts behavioral performance on spatial and feature attention tasks. Brain Research. 2006; 1080:63–72. [PubMed: 16412994]

Gould IC, Rushworth MF, Nobre AC. Indexing the graded allocation of visuospatial attention using anticipatory alpha oscillations. Journal of Neurophysiology. 2011; 105:1318–1326. [PubMed: 21228304]

Guerreiro MJ, Van Gerven PW. Now you see it, now you don't: evidence for age-dependent and age-independent cross-modal distraction. Psychology and aging. 2011; 26:415–426. [PubMed: 21443358]

Hanslmayr S, Gross J, Klimesch W, Shapiro KL. The role of alpha oscillations in temporal attention. Brain Research Reviews. 2011; 67:331–343. [PubMed: 21592583]

Hasher, L.; Zacks, RT. Working memory, comprehension, and aging: A review and a new view. In: Bower, GH., editor. The psychology of learning and motivation Advances in research and theory. Academic Press; 1988. p. 193-225.

Hillyard SA, Anllo-Vento L. Event-related brain potentials in the study of visual selective attention. Proceedings of the National Academy of Sciences of the United States of America. 1998; 95:781–787. [PubMed: 9448241]

Huang J, Sekuler R. Distortions in recall from visual memory: two classes of attractors at work. Journal of vision. 2010; 10 24.1–27.

Händel BF, Haarmeier T, Jensen O. Alpha Oscillations Correlate with the Successful Inhibition of Unattended Stimuli. Journal of Cognitive Neuroscience. 2010; 23:2494–2502. [PubMed: 20681750]

Jensen O, Mazaheri A. Shaping functional architecture by oscillatory alpha activity: gating by inhibition. Frontiers in human neuroscience. 2010; 4:186. [PubMed: 21119777]

Jost K, Bryck RL, Vogel EK, Mayr U. Are Old Adults Just Like Low Working Memory Young Adults? Filtering Efficiency and Age Differences in Visual Working Memory. Cerebral Cortex. 2011; 21:1147–1154. [PubMed: 20884722]

Kelly SP, Lalor EC, Reilly RB, Foxe JJ. Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. Journal of neurophysiology. 2006; 95:3844–3851. [PubMed: 16571739]

Klimesch W. EEG alpha and theta oscillations reflect cognitive and memory performance: a review and. Brain Research Reviews. 1999; 29:169–195. [PubMed: 10209231]

Lavie N, Fox E. The role of perceptual load in negative priming. Journal of Experimental Psychology: Human Perception and Performance. 2000; 26:1038–1052. [PubMed: 10884008]

Linkenkaer-Hansen K, Nikulin VV, Palva S, Ilmoniemi RJ, Palva JM. Prestimulus Oscillations Enhance Psychophysical Performance in Humans. J Neurosci. 2004; 24:10186–10190. [PubMed: 15537890]

Luck S, Woodman G, Vogel E. Event-related potential studies of attention. Trends in Cognitive Sciences. 2000; 4:432–440. [PubMed: 11058821]

Mathewson KE, Gratton G, Fabiani M, Beck DM, Ro T. To See or Not to See: Prestimulus {alpha} Phase Predicts Visual Awareness. J Neurosci. 2009; 29:2725–2732. [PubMed: 19261866]

May CP, Hasher L, Kane MJ. The role of interference in memory span. Memory & cognition. 1999; 27:759–767.

Mo J, Schroeder CE, Ding M. Attentional modulation of alpha oscillations in macaque inferotemporal cortex. Journal of Neuroscience. 2011; 31:878–882. [PubMed: 21248111]

Oostenveld R, Fries P, Maris E, Schoffelen J-M. FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. Computational intelligence and neuroscience. 2011; 2011:156869. [PubMed: 21253357]

Palva S, Palva JMM. New vistas for alpha-frequency band oscillations. Trends Neurosci. 2007; 30:150–158. [PubMed: 17307258]

Paxton JLL, Barch DMM, Racine CAA, Braver TSS. Cognitive Control, Goal Maintenance, and Prefrontal Function in Healthy Aging. Cereb Cortex. 2007

Rajagovindan R, Ding M. From prestimulus alpha oscillation to visual-evoked response: an inverted-U function and its attentional modulation. Journal of cognitive neuroscience. 2011; 23:1379–1394. [PubMed: 20459310]

Ray WJ, Cole HW. EEG alpha activity reflects attentional demands, and beta activity reflects emotional and cognitive processes. Science (New York, NY). 1985; 228:750–752.

Rohenkohl G, Nobre AC. Alpha Oscillations Related to Anticipatory Attention Follow Temporal Expectations. The Journal of Neuroscience. 2011; 31:14076–14084. [PubMed: 21976492]

Romei V, Gross J, Thut G. On the Role of Prestimulus Alpha Rhythms over Occipito-Parietal Areas in Visual Input Regulation: Correlation or Causation? The Journal of Neuroscience. 2010; 30:8692–8697. [PubMed: 20573914]

Rugg MD, Milner AD, Lines CR, Phalp R. Modulation of visual event-related potentials by spatial and non-spatial visual selective attention. Neuropsychologia. 1987; 25:85–96. [PubMed: 3574653]

De Sanctis P, Gomez-Ramirez M, Sehatpour P, Wylie GR, Foxe JJ. Preserved executive function in high-performing elderly is driven by large-scale recruitment of prefrontal cortical mechanisms. Human Brain Mapping. 2009; 30:4198–4214. [PubMed: 19572310]

Sander MC, Werkle-Bergner M, Lindenberger U. Amplitude modulations and inter-trial phase stability of alpha-oscillations differentially reflect working memory constraints across the lifespan. NeuroImage. 2011; 59:646–654. [PubMed: 21763439]

Sauseng P, Hoppe J, Klimesch W, Gerloff C, Hummel FC. Dissociation of sustained attention from central executive functions: local activity and interregional connectivity in the theta range. European Journal of Neuroscience. 2007; 25:587–593. [PubMed: 17284201]

Sauseng P, Klimesch W, Heise KF, Gruber WR, Holz E, Karim AA, Glennon M, Gerloff C, Birbaumer N, Hummel FC. Brain Oscillatory Substrates of Visual Short-Term Memory Capacity. Current Biology. 2009; 19:1846–1852. [PubMed: 19913428]

Snyder AC, Foxe JJ. Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: a high-density electrical mapping study. The Journal of Neuroscience: The Official Journal of the Society for Neuroscience. 2010; 30:4024–4032. [PubMed: 20237273]

Thut G, Nietzel A, Brandt SA, Pascual-Leone A. Alpha-band electroencephalographic activity over occipital cortex indicates visuospatial attention bias and predicts visual target detection. Journal of Neuroscience. 2006; 26:9494–9502. [PubMed: 16971533]

Vallesi A, McIntosh AR, Stuss DT. Overrecruitment in the Aging Brain as a Function of Task Demands: Evidence for a Compensatory View. Journal of Cognitive Neuroscience. 2010:1–15. [PubMed: 19199421]

Vogel EK, McCollough AW, Machizawa MG. Neural measures reveal individual differences in controlling access to working memory. Nature. 2005; 438:500–503. [PubMed: 16306992]

Vogel EKE, Machizawa MGM. Neural activity predicts individual differences in visual working memory capacity. Nature. 2004; 428:748–751. [PubMed: 15085132]

Weissman D, Roberts K, Visscher K, Woldorff M. The neural bases of momentary lapses in attention. Nature neuroscience. 2006; 9:971–978.

Yotsumoto Y, Sekuler R. Out of mind, but not out of sight: intentional control of visual memory. Memory cognition. 2006; 34:776–786. [PubMed: 17063909]

Zanto TP, Hennigan K, Ostberg M, Clapp WC, Gazzaley A, Östberg M. Predictive knowledge of stimulus relevance does not influence top-down suppression of irrelevant information in older adults. Cortex; a journal devoted to the study of the nervous system and behavior. 2010; 46:564–574.

Zanto TP, Pan P, Liu H, Bollinger J, Nobre AC, Gazzaley A. Age-related changes in orienting attention in time. The Journal of neuroscience : the official journal of the Society for Neuroscience. 2011; 31:12461–12470. [PubMed: 21880908]

Highlights

- We study the neural mechanisms younger and older adults use to ignore stimuli.
- Here, younger and older adults both successfully ignored irrelevant stimuli.
- Younger adults use increased alpha power to suppress irrelevant stimuli.
- Suppressing stimulus processing in older adults does not require alpha modulation.
- When older adults filter inputs they use different strategies than younger adults.

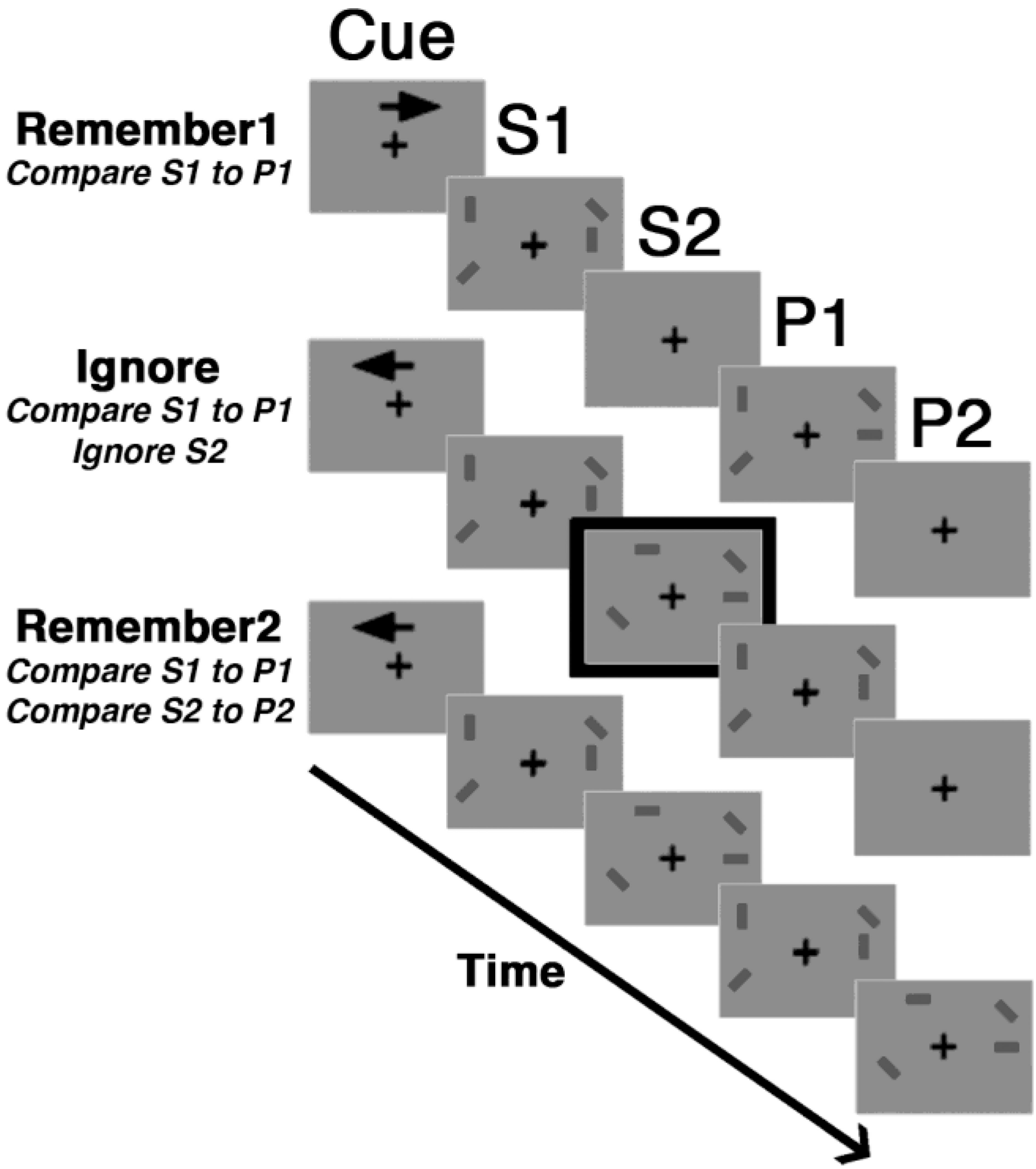

Figure 1. Short-Term Memory Task (Change Detection)

At the start of each trial, a cue was presented (200ms) to inform the participants whether the left or right side of stimuli would be relevant. The stimuli (S1 and S2) were presented for 100ms each. The probes (P1 and P2) were presented until response or 2000ms. Participants responded with a button press indicating whether P1 (or P2) matched S1 (or S2). When the probe differed from the stimulus, only one of the oriented bars was changed: its orientation was shifted by 90 degrees (example of ‘different’ trial is seen in top row – *Remember1*). There were random delays of 700–1200ms between stimulus onsets. The black frame highlights the stimulus (S2) participants were instructed to ignore in the *Ignore* condition.

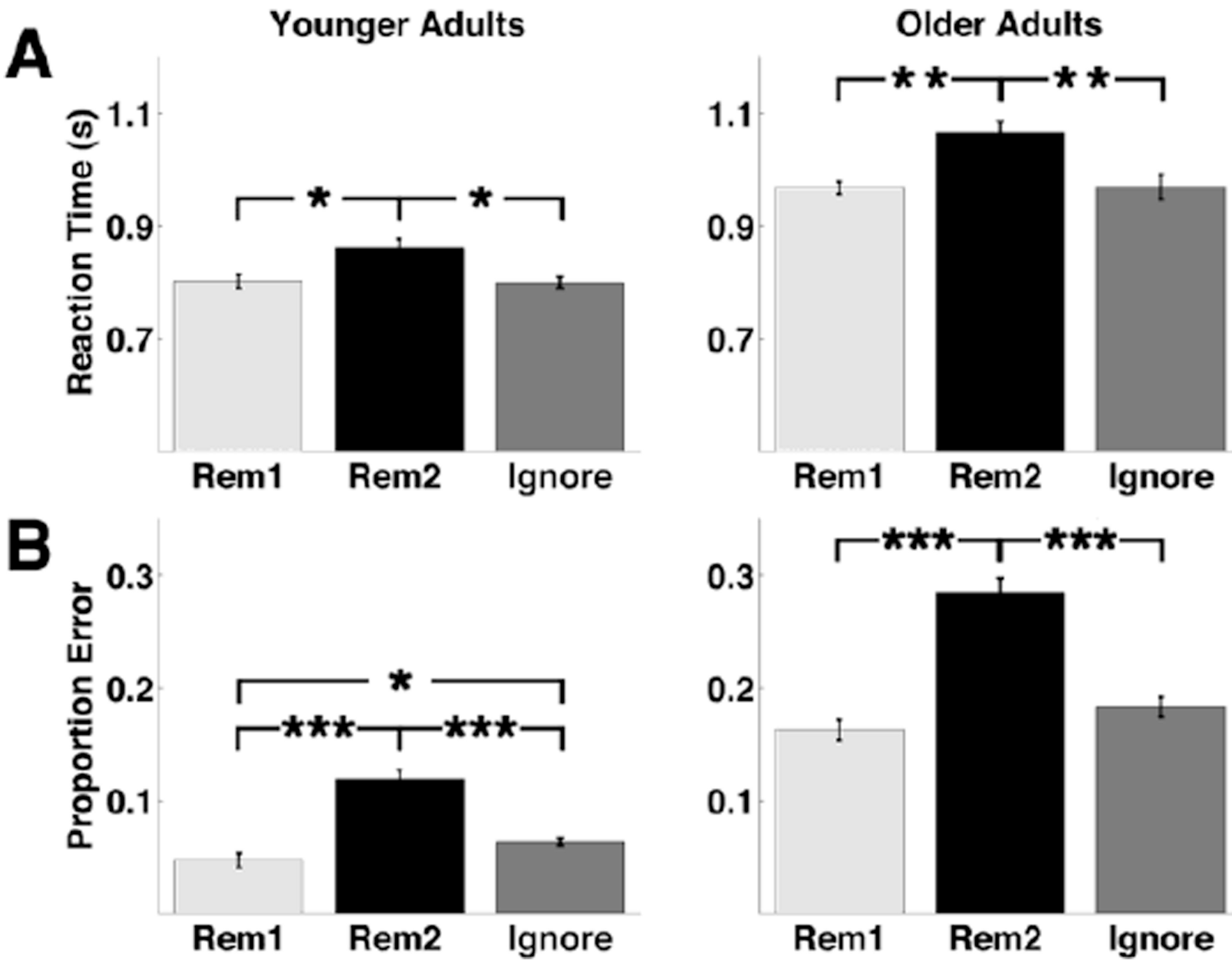

Figure 2. Behavioral evidence that older adults suppress distracting information

Although older adults had slower reaction times and made more errors, both groups performed well when asked to remember only one stimulus (*Rem1*). Remembering two stimuli (*Rem2*) was more difficult for both younger and older adults, resulting in more errors ($p<0.001$) and slower reaction times (younger $p=0.050$, older $p=0.0011$). However, when instructed to ignore the second stimulus (*Ignore*), performance improved dramatically: reaction time for both younger adults ($p=0.87$) and older adults ($p=0.96$) and proportion error for older adults were statistically indistinguishable between *Remember1* and *Ignore* ($p=0.16$). This implies that, in the *Remember2* condition, remembering the second stimulus interfered with the memory of the first, and that ignoring a second stimulus reduced this interference.

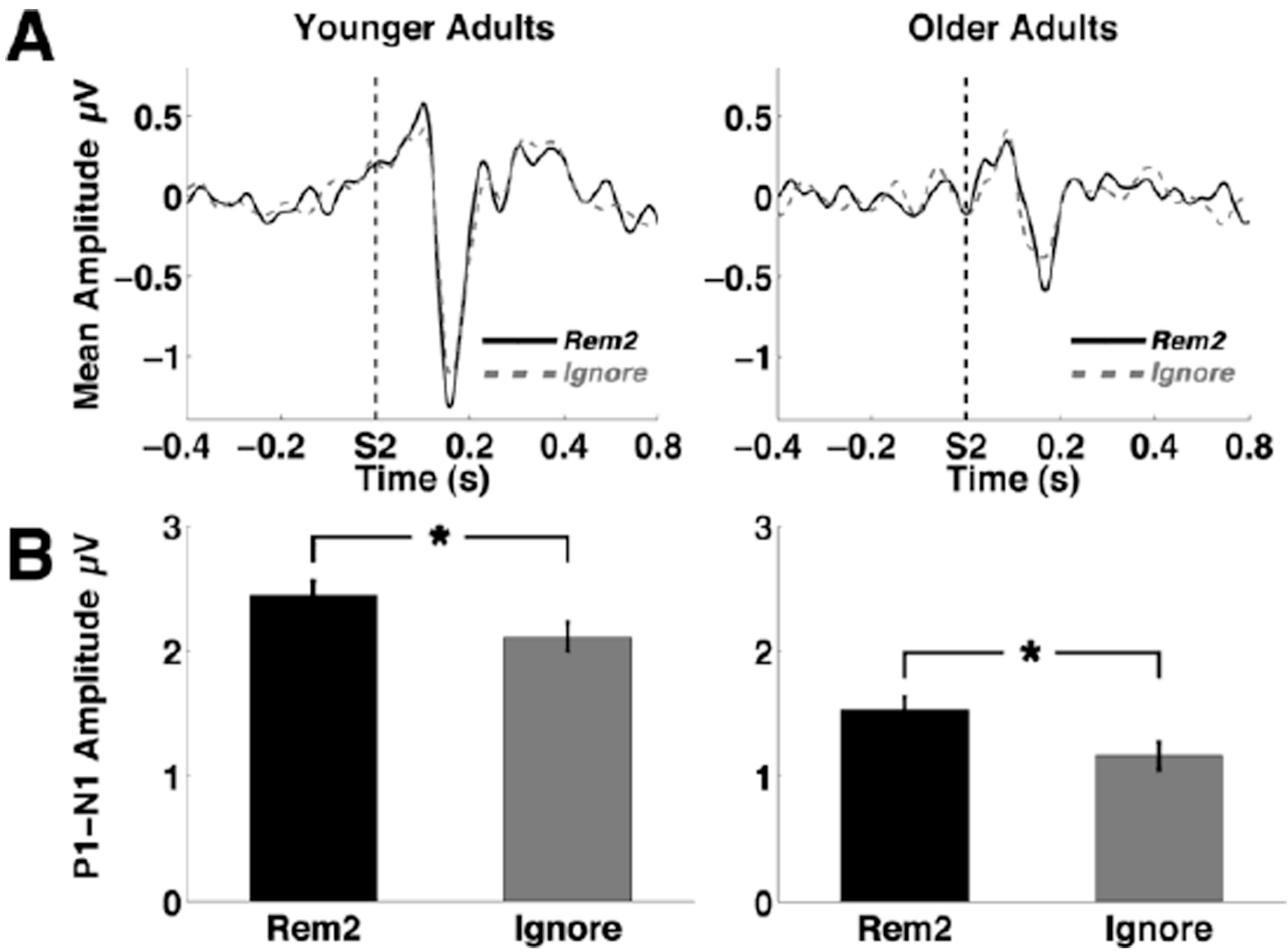

Figure 3. ERP evidence that older adults suppress distracting information

(A.) Mean ERP for *Ignore* (gray dashed) and *Remember2* (black) conditions. Stimulus onset occurred at timepoint zero (S2). The difference between the P1 and N1 peaks reflects modulation of attention between the conditions. Mean represents electrodes P1, P2, P3, and P4, averaged across all participants (B.) P1-N1 amplitude for *Remember2* (black) and *Ignore* (gray) conditions for younger adults and older adults (calculated as difference between P1 and N1 peak for each participant, in order that slight variations in timing would not affect the results). The mean ERP amplitude is significantly different between conditions for younger ($p=0.035$) and older adults ($p=0.032$). The interaction between the younger and older adults ERP modulation was not significant (task X group $p=0.17$).

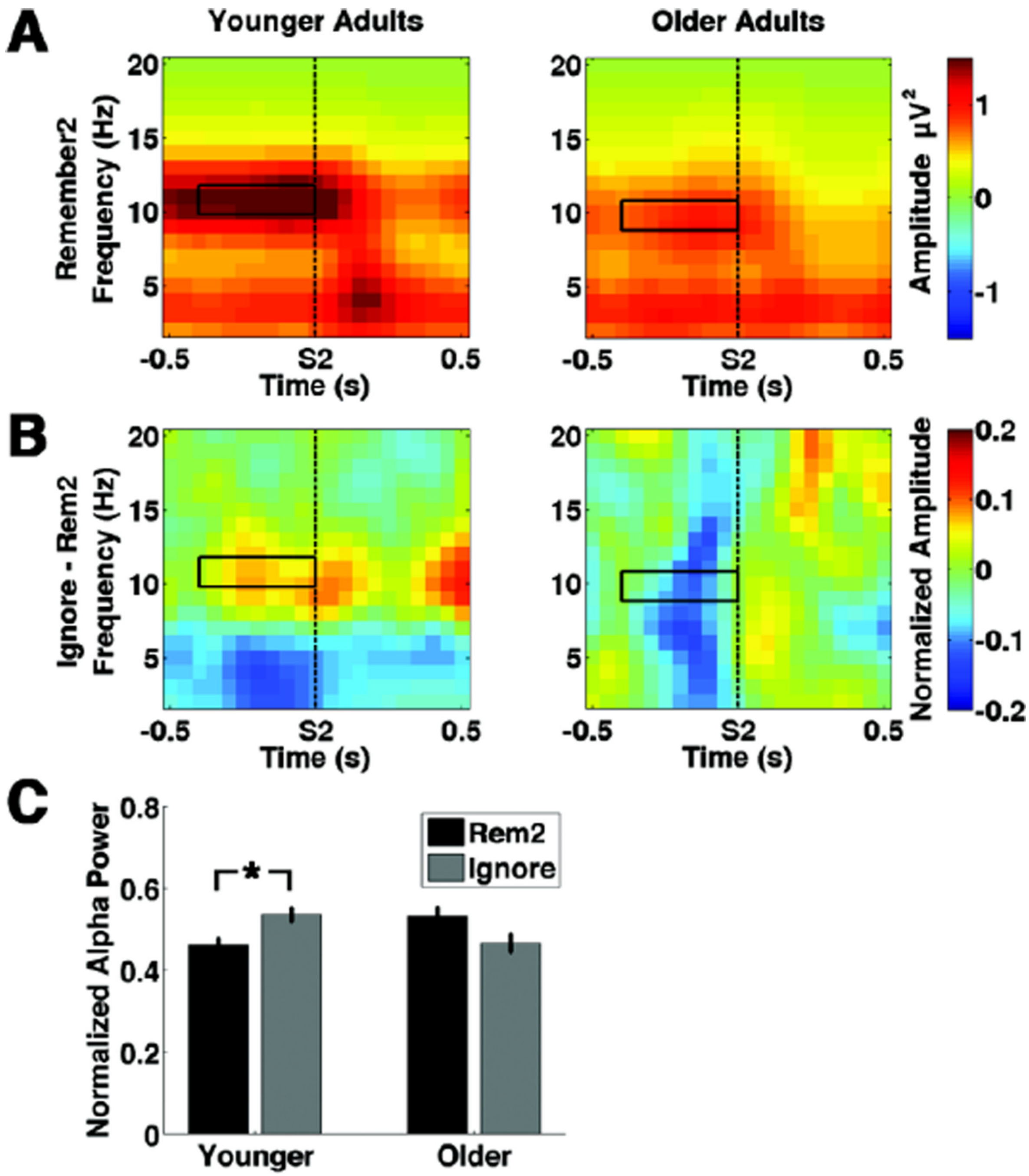

Figure 4. Comparison of prestimulus alpha between *Ignore* and *Remember2* conditions

Stimulus onset is represented by time zero (S2). (**A**.) Raw time-frequency plots during ignore trials only (*Ignore*). Older adults show less power in the alpha band than younger adults. (**B**.) During the period when the participant anticipates the stimulus, younger adults modulate alpha power as predicted (normalized value: *Ignore – Remember2 / Ignore + Remeber2*). NOTE: Box is centered on mean alpha peak for age group (younger adults 10.8Hz and older adults 9.8Hz) during the period just prior to stimulus (S2) presentation (0 to −400ms). (**C**.) Younger adults showed significant modulation between conditions: more alpha power when instructed to ignore than to remember (p=0.039). The interaction of task by group is significant (p=0.017). NOTE: Plot represents alpha defined by individual subjects' peaks, though the qualitative results do not depend on this choice.

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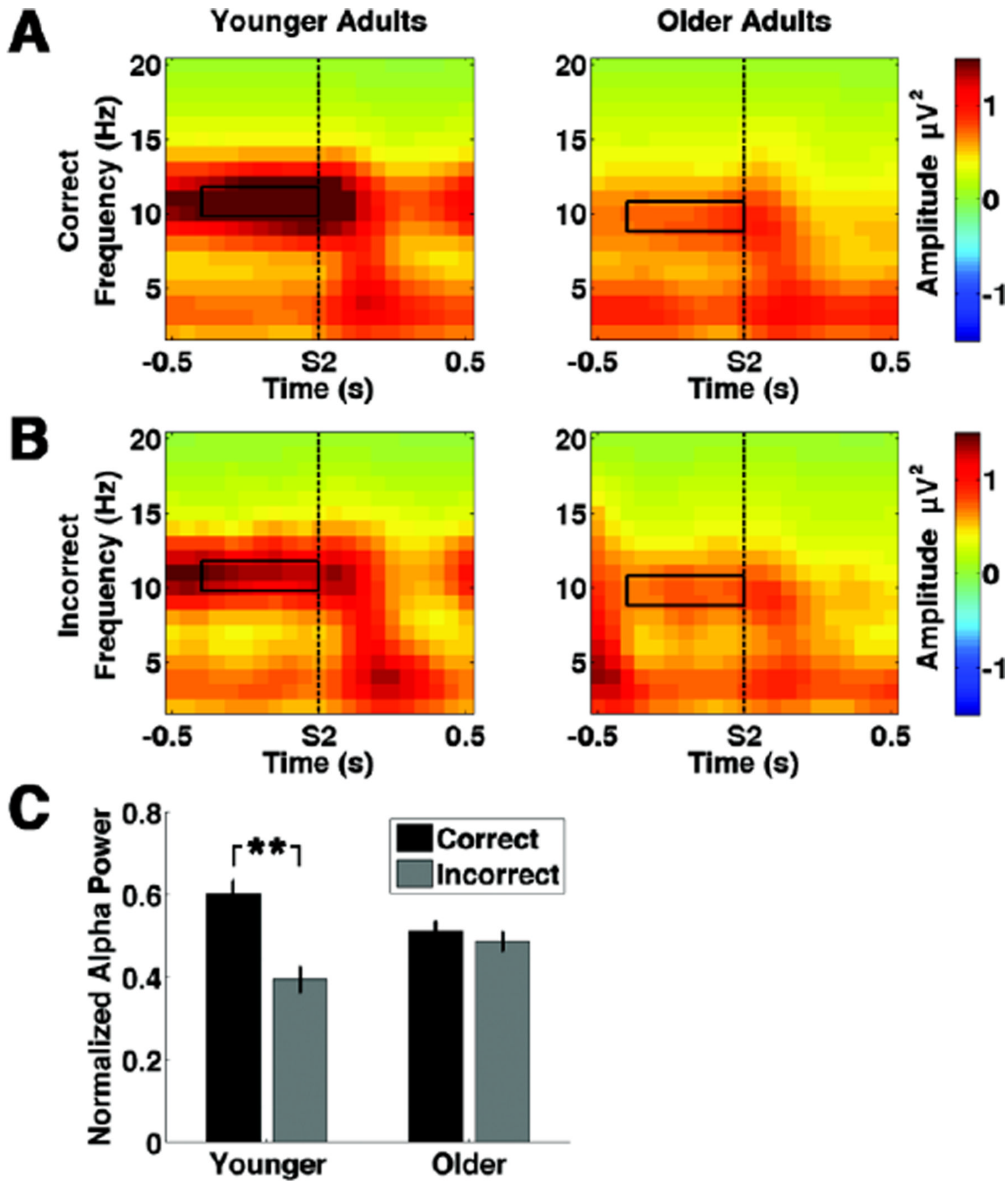

Figure 5. Comparison of prestimulus alpha between correct and incorrect *Ignore* trials

Stimulus onset is represented by time zero (S2). Younger adults show significant difference in alpha power between correct and incorrect *Ignore* trials (p=0.0035). More prestimulus alpha power is correlated with successful suppression of irrelevant information in younger adults, but not for older adults (p>0.05). The interaction of group by task is significant (p=0.030). (**A**.) Prestimulus alpha power for correct Ignore trials for younger adults and older adults. (**B**.) Prestimulus alpha power for incorrect Ignore trials for younger adults and older adults. (**C**.) Normalized alpha power for correct and incorrect trials for younger adults and older adults.