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Predictive cues and age-related declines in working memory performance

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Abstract

Older adults, compared to younger adults, do not benefit from predictive information regarding either what type of stimuli they will see or when to expect them, yet it is unclear whether older adults benefit when given both types of predictive information. Here, electroencephalogram recordings of older (aged 62–87) and younger (aged 20–32) adults were recorded during a working memory task. Each trial contained two faces and two scenes presented sequentially, followed by a 5-second delay and a probe stimulus. Participants were told what stimuli to remember/ignore and when they would appear. Predictive cues enabled older adults to remember stimuli as accurately as younger adults, though response times were significantly slower, even when corrected for general age-related slowing. Previously observed reductions in P1/N1 amplitude and latency suppression to irrelevant stimuli were not seen. Rather, older adults exhibited lowered P3 amplitudes to relevant stimuli; those with the greatest declines yielded the lowest accuracy and slowest response times. This shows that predictive information can help maintain accuracy, though not response times which correspond to age-related declines in neural enhancement to relevant stimuli.

Keywords

EEG; aging; P3 amplitude; working memory; enhancement deficit; predictive information

1 INTRODUCTION

It is widely known that older adults experience performance deficits in tasks of working memory compared to younger adults (Foos, 1989; McEvoy et al., 2001; Wingfield et al., 1988). Although these deficits were previously thought to be caused by a smaller working memory capacity in older adults (Kahneman, 1973), subsequent research has identified reduced attentional capacity in older adults (Craik & Byrd, 1982). More recent studies relating to the inhibitory deficit hypothesis have shown that the inability to ignore goal-

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irrelevant information may contribute to overloading limited cognitive resources in older adults, resulting in multiple declines, including working memory deficits (Hasher et al., 2007, 1999). Indeed, when older adults are given working memory tasks with high levels of distraction, they perform worse compared to tasks with low levels of distractions both for visual (Lustig et al., 2006; Tipper, 1991) and auditory tasks (McDowd and Filion, 1992). Alternatively, the processing speed hypothesis of cognitive aging relates poor cognitive performance to slowed information processing which necessitates allocating more time toward information encoding (Salthouse, 1996). The delayed processing then limits the content that can be processed in later-stages of neural processing, which can result in working memory declines in aging (Salthouse, 1991; Zanto et al., 2010a). Together, it appears that the combined inability to suppress neural activity to irrelevant information and slowed neural processing both contribute to cognitive declines in aging (Gazzaley et al., 2008; Zanto and Gazzaley, 2014).

In order to better ignore distracting information in tasks involving high working memory demands, it may be hypothesized that predictive cues may be used to guide attention toward relevant, as well as away from irrelevant, information. It has been known for over a hundred years that predictive cues may enhance performance abilities (Woodrow, 1914). In both primates (Chelazzi et al., 1993; Luck et al., 1997) and humans (Bollinger et al., 2010; Gazzaley et al., 2005a; Giesbrecht et al., 2006; Hopfinger et al., 2000), predictive cue information directs attention toward relevant stimuli by increasing the magnitude and speed of neural activity in visual cortical regions that are selective for the attended stimuli, and this biasing of neural activity corresponds to improved behavioral performance. However, older adults' working memory performance is not improved as it is in youth when presented with predictive cues. Specifically, older adults do not suppress visual cortex activity related to processing goal-irrelevant information, which would otherwise benefit performance, when given predictive cues that identify what type of stimuli is relevant (Gazzaley et al., 2005, Gazzaley et al., 2008, Chadick et al., 2014) or when the relevant stimuli will appear (Zanto et al., 2010). In response to irrelevant information, older adults exhibit greater blood oxygen level dependent (BOLD) signal (i.e., less suppression) than younger adults within sensory cortex, which correlate with working memory deficits (Gazzaley et al., 2005; Chadick et al., 2014). Importantly, this age-specific suppression deficit is observed although enhancement of neural activity to relevant stimuli is intact (Gazzaley et al., 2005; Chadick et al., 2014). Similarly, when provided cues to what stimuli will be relevant, or when the relevant stimuli will appear, electroencephalography (EEG) data from older adults demonstrate deficits in suppressing neural activity during early processing stages such that irrelevant faces yield larger P1 amplitude and speeded N1 latency, which more closely resembles neural processing to relevant stimuli (Gazzaley et al., 2008; Zanto et al., 2010). Together, these data suggest older adults' working memory performance does not benefit from cues that provide predictive information regarding what is relevant or when the relevant stimuli will appear, and this is marked by deficient suppression of neural activity to irrelevant information.

Yet, to fully anticipate a future event, information regarding what, where, and when to expect the event is required. Therefore, it is unclear whether older adults may benefit from additional predictive cues that provide information on both what type of stimuli are relevant and when the relevant stimuli will appear (and where is known a priori). In order to better understand how older adults may engage attentional mechanisms to yield successful working memory performance, younger and older adults in the present paradigm were provided with full predictive information regarding stimulus presentation.

Twenty-one healthy older adults and twenty healthy younger adults engaged in a delayed recognition paradigm that incorporated predictive cue information at the beginning of each trial. The paradigm was designed to examine whether older adults can effectively utilize complex predictive cues to yield comparable working memory performance as well as comparable measures of neural activity suppression to irrelevant stimuli as younger adults. Predictive cue information instructed participants on the type of stimuli that were relevant as well as when the relevant stimuli were presented. It was hypothesized that such informative cues may enable older adults to suppress distraction caused by irrelevant stimuli and consequently exhibit working memory performance comparable to younger adults. Electroencephalography (EEG) measures were recorded during the experiment and event-related potentials (ERPs) were analyzed to determine differences in neural activity associated with behavioral performance within and between the age groups. The ERP components of interest included the P1, N170 (N1), and P3, as these have been previously shown to be modulated by attention and have been associated with an age-related suppression deficit to irrelevant faces (Gazzaley et al., 2008, 2005a; Zanto et al., 2010). As the goal of the study was to address age-related differences in processing and subsequent working memory performance, face stimuli were chosen for analysis due to the utility and sensitivity of EEG in detecting neural activity related to face processing (Bentin et. al., 1996, Herrmann et. al., 2005), and the previous association with age-related suppression deficits (Gazzaley et al., 2008, 2005a; Zanto et al., 2010).

2 METHODS

2.1 Participants

Twenty younger (Mean age = 25 years; Range = 20–32 years; Males = 10) and twenty-one older (Mean age = 72 years; Range = 62–87 years; Males = 8) adults gave consent to participate in the study. All participants were screened to ensure that they were in normal health, had no history of neurological, psychiatric, or vascular disease, were not depressed, and were not taking any psychotropic or hypertensive medications. All participants had normal to corrected vision and were right handed. One older participant was excluded due to excessive EEG artifacts, resulting in 20 younger and 20 older participants.

2.2 Neuropsychological Testing

Participants in the older age group were administered 11 neuropsychological tests of executive and memory function, and were found to be cognitively intact (within two standard deviations) relative to normative values from age-matched controls. Neuropsychological testing was performed on a separate day from EEG and included the following tests: MMSE, geriatric depression (GDS), visual-spatial function (modified Rey-Osterrieth), visual-episodic memory (memory for details of a modified Rey-Osterrieth Complex Figure), visual-motor sequencing (trail making test B), Logical Memory I, Verbal Paired Associates I, and Visual Reproduction II (all from the Weschler Memory Scale

Revised), the California Verbal Learning Test (CVLT), stroop interference, WAIS-R backward digit span, and WAIS digit symbol test. Group scores for these tests and demographic data on participants are presented in Table 1.

2.3 Stimuli

The stimuli consisted of grayscale images of faces and natural scenes. Each face and scene image presented during the experiment was unique (i.e., images were not repeated in different trials). Images were 225 pixels wide and 300 pixels tall, (14 × 18 cm) and subtended approximately 5 by 6 degrees of visual angle (participants were approximately 172 cm from the screen). The face stimuli consisted of a variety of neutral-expression male and female faces across a large age range. The gender of the face stimuli was held constant within each trial.

2.4 Experimental Procedure

The cognitive paradigm was composed of six different tasks per stimulus type to be remembered (faces and scenes) as well as one passive viewing task (Figure 1). Each task consisted of the same basic temporal design, such that they all required viewing four images (encode period): two faces and two scenes each being displayed for 800 msec (200 msec inter-stimulus interval), followed by a 5 sec delay period in which the relevant images were to be maintained in working memory. After the delay, a fifth image appeared (probe) for 1 sec. Participants were asked to respond with a button press as quickly as possible without sacrificing accuracy, whether the probe image matched either of the two relevant images held in memory (match or no match). For the Face Memory task, the participants were asked to remember only the face stimuli and to ignore the scene stimuli; for the Scene Memory task, the participants were asked to remember only the scene stimuli and to ignore the face stimuli. During the Passive View task, participants were instructed to relax and view the stimuli without trying to remember them, and instead of a probe image, an arrow was presented where participants were required to make a button press indicating the direction of the arrow (left or right).

The memory tasks were presented in 12 blocks (6 each for faces and scenes) in which participants were informed about which stimuli were relevant by the order of their appearance: positions 1 & 2, 1 & 3, 1 & 4, 2 & 3, 2 & 4, or 3 & 4. Both the relevant stimuli were of the same stimulus type, meaning that during Face Memory, the two cued positions (e.g., 1 & 2) were both relevant faces. The probe stimulus matched a previously presented stimulus during the encode period on 50% of the trials (randomized). Participants were presented with a task reminder at the beginning of each trial until a button was pressed to initiate the trial. For example, at the beginning of a trial, participants were presented the text “Faces 1 & 2”, which instructed them to remember the relevant faces that would appear at positions 1 & 2 (i.e., first and second stimuli out of the four presented), and thus, ignore the irrelevant scenes that would appear at positions 3 & 4. The passive viewing task was presented across 4 task blocks while the 12 memory task blocks (6 per stimulus type) were each presented in separate blocks. Thus, 16 total task blocks were presented during the experiment and the order of presentation was randomized across participants. All participants received 6 blocks of 18 trials each for the Scene Memory task, leading to 108 trials and 216 epochs of data each from attended scenes and ignored faces. All participants also received 6 blocks of 12 trials each for the Face Memory task, leading to 72 trials and 144 epochs of data each from attended faces and ignored scenes. Participants also received 4 blocks of 18 trials each for the Passive view task, leading to 72 trials and 144 epochs of data each from passively viewed faces and scenes. The number of trials was weighted toward the Scene Memory task because previous research demonstrated a selective age-related deficit in suppressing neural activity to ignored faces as recorded by EEG (Gazzaley et. al. 2008, Zanto et. al. 2010). Thus, there were more Scene Memory task trials to ensure sufficient power for assessing the effects of predictive information on the previously observed age-based suppression deficit to faces.

2.5 Data acquisition

Participants sat in an armchair in a dark, sound-attenuated room and were monitored by a camera during all tasks. EEG data were recorded during all 16 task blocks. Electrophysiological signals were recorded with an ActiveTwo 64-channel Ag–AgCl active electrode EEG acquisition system (BioSemi) in conjunction with ActiView software (BioSemi). Signals were amplified and digitized at 1024 Hz with a 24-bit resolution. All electrode offsets were maintained between ±20 mV.

2.6 Data analysis

Behavioral responses more than 2 standard deviations away from the participant’s mean response time were excluded from analysis (5.1% of total trials). The goal of the study was to address age-related differences in face processing and subsequent working memory performance. Only face stimuli were chosen in order to select electrodes for statistical analyses and because the electrodes of interest for face stimuli are well characterized (Bentin et. al., 1996, Herrmann et. al., 2005, Gazzaley et. al., 2008, Zanto et. al., 2010). Therefore, EEG analyses focused on the attended face stimuli from the Face Memory task, the ignored face stimuli from the Scene Memory task, and the passively viewed face stimuli from the Passive View task. All data processing was conducted in Matlab (The Mathworks, Inc.). Raw EEG data were referenced to the average off-line. Bad electrodes were visually identified and corrected using spherical spline interpolation prior to re-referencing to the average. Data were filtered between 1 and 30 Hz using a finite impulse response filter and then epochs were extracted from the filtered data beginning 200 msec pre-stimulus onset and ending 1000 msec post-stimulus onset. The pre-stimulus baseline was subtracted from each epoch and a voltage threshold of ±50 μV was used to reject epochs containing artifacts prior to calculating the ERP. Electrodes of interest were selected for statistical analysis consistent with previous reports (Gazzaley et al., 2008; Zanto et al., 2010) and the topography of the ERP. Electrodes of interest for the P1 and the N1 were averaged over PO7, P7, P9, and O1 for the left hemisphere and PO8, P8, and P10, and O2 for the right hemisphere. The electrode of interest for the P3 was POZ. To account for the unequal number of epochs between the attended and ignored faces, ERPs were bootstrapped prior to statistical analyses. As there were 30 more trials (i.e., 72 more epochs) of ignored faces than attended and passively viewed faces, the trials of ignored faces were bootstrapped to allow for equal sample sizes. The bootstrapping procedure consisted of a random sampling of trials from the larger data sets to equate the number of trials from the smaller data set and then used to calculate a sample ERP. This process was iterated 5000 times and the bootstrapped ERP was calculated from the 5000 sample ERPs. Peak P1 values were chosen as the largest amplitude between 50 and 150 msec post-stimulus onset, and the N1 was identified as the most negative amplitude between 120 and 220 msec. P1 and N1 amplitudes were averaged ±5 msec around the peak prior to statistical analysis whereas P3 amplitudes were calculated as the average amplitude value between 300 and 500 msec post-stimulus onset. Additional analyses included frontal cortex activity as an average amplitude value between 300 and 500 msec post-stimulus onset using Fz and FCz as electrodes of interest. Additionally, later P3 activity was assessed between 500 and 700 msec post-stimulus onset. Statistical analysis for the ERP consisted of an analysis of variance (ANOVA) with a Greenhouse–Geisser correction applied when appropriate. All post-hoc t-tests were corrected by the false discovery rate method.

3 RESULTS

3.1 Behavioral performance

Working memory accuracy and response times were compared between older and younger adults using ANOVAs with Age (younger, older) and Stimulus Type (face, scene) as factors. Results for working memory accuracy indicated no main effect of Age ($F(1,38) = 0.04$, $p = 0.85$, $\eta_p^2 = 0.001$). There was a main effect of Stimulus Type ($F(1,38) = 40.98$, $p < 0.01$, $\eta_p^2 = 0.52$) indicating working memory accuracy for scenes was lower than for faces, but no interaction between Age and Stimulus Type ($F(1,38) = 0.34$, $p = 0.56$, $\eta_p^2 = 0.0088$; Figure 2a) was observed.

To correct for age-related motoric slowing, response times during the working memory tasks were normalized by subtracting response times from the Passive View task. Normalized response time performance showed a main effect of Age ($F(1,38) = 11.47$, $p < 0.01$, $\eta_p^2 = 0.23$; Figure 2b), such that older adults responded slower than younger adults and a main effect of Stimulus Type ($F(1,38) = 26.28$, $p < 0.001$, $\eta_p^2 = 0.41$) indicating responses were slower to scene stimuli compared to face stimuli. There was no interaction between Age and Stimulus Type ($F(1,38) = 0.00$, $p = 0.96$). In sum, these results show an age-related decline in working memory performance in terms of slower response times, which may not be attributed to general age-related slowing or diminished accuracy.

3.2 Electrophysiological measures

ERP analyses focused on the P1, N1, and P3. Figure 3 highlights P1 and N1 related ERP data subjected to analysis for both younger (Figure 3a) and older (Figure 3b) adults, averaged across both hemispheres. Amplitude and latency measures from the P1 and N1 were submitted to ANOVAs with Task (attend, passive, ignore), Age (younger, older), and Hemisphere (left, right) as factors. Results for the P1 amplitude showed no significant main effects or interactions. The ANOVA for the P1 latency also displayed no main effects, but did exhibit an Age × Task interaction ($F(2,76) = 3.74$, $p < 0.05$, $\eta_p^2 = 0.09$). To investigate the Age × Task interaction, two-tailed *t*-tests were conducted to assess age-related differences in top-down enhancement (attend – passive), suppression (ignore – passive), and attentional modulation (attend – ignore). Between group comparisons of the P1 latency suppression

($t(38) = 1.43$, $p = 0.52$), P1 latency enhancement ($t(38) = 0.96$, $p= 0.22$), and P1 latency attentional modulation ($t(38) = 1.6$, $p = 0.22$) showed no age-related effects. However, this Age × Task interaction was driven by P1 latency attentional modulation when not correcting for multiple comparisons ($t(38) = 1.6$, $p = 0.22$, corrected, $p < 0.05$, uncorrected) such that older adults exhibited slower P1 latency when faces were attended compared to ignored ($t(19) = 2.50$, $p < 0.05$, uncorrected) and younger adults did not exhibit latency differences between attended and ignored stimuli ($t(19) = 0.36$, $p > 0.05$, uncorrected). No other main effects or interactions were observed for the P1 latency.

Analysis of the N1 amplitude resulted in a main effect of Age ($F(1,38) = 5.39$, $p < 0.05$, $\eta_p^2 = 0.12$) such that younger adults had smaller N1 amplitudes than older adults. The ANOVA for the N1 amplitude also displayed a main effect of Task ($F(2,76) = 3.55$, $p < 0.05$, $\eta_p^2 = 0.09$) as participants exhibited the most negative N1 amplitudes when attending to the stimuli and the least negative N1 amplitudes when ignoring the stimuli. No other main effects or interactions were observed for the N1 amplitude.

Analysis of the N1 latency also exhibited a main effect of Age ($F(1,38) = 24.3$, $p < 0.001$, $\eta_p^2 = 0.39$) indicating that older adults' N1 peaked slower than younger adults. The N1 latency ANOVA also displayed an Age × Hemisphere interaction ($F(1,38) = 7.89$, $p < 0.01$, $\eta_p^2 = 0.17$). Whereas the N1 in older adults was speeded in the right hemisphere compared to their left hemisphere ($t(19) = 2.47$, $p < 0.05$), the opposite was true in younger adults though not significant ($t(19) = 0.66$, $p = 0.51$). No other main effects or interactions were observed for the N1 latency. Though the N1 amplitude and latency measures displayed an aging effect, there were no attention-related aging effects (i.e. no differences in enhancement, suppression, or attentional modulation for N1 amplitude or latency).

P3 amplitude data was then subjected to analysis for both younger (Figure 3c) and older (Figure 3d) adults. Amplitude measures from the P3 were submitted to an ANOVA with Task (attend, passive, ignore) and Age (younger, older) as factors. Results indicated a main effect of Task ($F(2,76) = 8.12$, $p < 0.001$, $\eta_p^2 = 0.17$) such that P3 amplitudes were greater when attending to relevant stimuli compared to ignoring irrelevant stimuli (i.e., attentional modulation; ($t(39) = 3.91$, $p < 0.01$) and passively viewing stimuli (i.e., enhancement; ($t(39) = 4.68$, $p = 0.0001$) but not when passively viewing stimuli compared to ignoring irrelevant stimuli (i.e., suppression; ($t(39) = 1.06$, $p = 0.29$). There was also an Age × Task interaction at the P3 amplitude ($F(2,76) = 4.08$, $p < 0.05$, $\eta_p^2 = 0.09$) showing that younger adults exhibited P3 amplitude enhancement (i.e., attend > passive; $t(19) = 2.94$, $p < 0.01$), but older adults did not exhibit such enhancement ($t(19) = 0.79$, $p = 0.43$). A direct comparison between groups showed a significant difference between P3 enhancement for older and younger adults ($t(38) = 2.08$, $p = 0.04$, Figure 4a).

The relationship between P3 amplitude enhancement and behavior was then analyzed for the older adults by dividing this group into two categories based on a median split of their P3 enhancement abilities. Accuracies and response times were then compared between these subgroups. Older adults exhibiting larger P3 enhancement yielded higher accuracy than older adults who did not exhibit P3 enhancement ($t(9) = 2.44$, $p < 0.01$; Figure 4b). Similarly, older adults with higher levels of P3 enhancement also responded faster than those who did not exhibit P3 enhancement ($t(19) = 2.03$, $p = 0.05$; Figure 4c). The relationship between P3 amplitude enhancement and task performance revealed no significant correlation for either age group (P3 enhancement and normalized response time in older: $r = -0.23$; $p = 0.33$ and younger: $r = -0.36$; $p = 0.11$; P3 enhancement and accuracy performance in older: $r = 0.43$; $p = 0.057$ and younger: $r = 0.38$; $p = 0.09$). The use of the median split is generally a more conservative approach, although it is not always appropriate, for example, when a conducting a correlation on data that has been dichotomized (MacCallum et al., 2002). However, the median split when coupled with t-tests as conducted here can identify subtle relationships between enhancement measures and behavioral performance because it is less sensitive to variance across the population.

To account for the possibility that the observed P3 amplitude effect resulted from a P3 latency shift in aging, a later time window was created extending from 500 msec to 700 msec after stimulus onset for both the younger and older adults. These P3 amplitude measures were submitted to an ANOVA with Task (attend, passive, and ignore) and Age (young, old) as factors. Results indicated a main effect of Task ($F(2,76) = 28.97$, $p < 0.0001$, $\eta_p^2 = 0.34$) such that for both older and younger adults, P3 amplitudes were greater when attending to relevant stimuli compared to ignoring irrelevant stimuli (Older: $t(19) = 6.13$, $p < 0.00001$; Younger: $t(19) = 4.19$, $p < 0.0001$) and passively viewing stimuli (Older: $t(19) = 5.10$, $p < 0.0001$; Younger: $t(19) = 4.64$, $p < 0.001$). There was also a main effect of Age ($F(1,38) = 4.03$, $p = 0.047$, $\eta_p^2 = 0.034$ such that younger adults had larger P3 amplitudes than older adults. No other main effects or interactions were observed for the P3 amplitude. Despite the lack of an Age × Task interaction, the magnitude of enhancement was compared between age groups and older adults exhibited lower enhancement compared to younger adults in this later P3 time window ($t(38) = 2.83$, $p < 0.01$; Figure 3 c, d). Figure 5 displays peak activity modulation (i.e., enhancement) with a topographical distribution centered around midline parietal regions for younger (Figure 5a) and older adults (Figure 5c) during the early P3 time window and for younger (Figure 5b) and older adults (Figure 5d) during the late P3 time window, demonstrating the extent of the enhancement deficit in aging over both time windows.

To assess whether later P3 enhancement related to task performance, older adults were again divided into two categories based on a median split of their later stage P3 enhancement abilities, and accuracies and normalized response times were then compared between these sub-groups. There was no significant difference in accuracy or normalized response time performance between older adults exhibiting higher levels of P3 enhancement and older adults with less P3 enhancement during this later time window. Of note, the relationship between P3 amplitude enhancement and task performance revealed no significant correlation for either age group (P3 enhancement and normalized response time in older: $r = -0.24$; $p = 0.29$ and younger: $r = -0.36$; $p = 0.11$; P3 enhancement and accuracy performance in older: $r = 0.43$; $p = 0.11$ and younger: $r = 0.38$; $p = 0.09$). Thus, only the early P3 (300–500ms) enhancement exhibited a relationship with working memory performance. Together these results indicate that an age-related decline in early P3 enhancement results in subsequent declines in working memory performance.

To assess whether older adults employed frontal compensation during the time period in which the posterior P3 enhancement deficit was the greatest (300 to 500 msec after stimulus onset), frontal electrode amplitude measures were examined for both younger adults (Figure 6a) and older adults (Figure 6b). Both fMRI (Stern 2002; Reuter-Lorenz & Lustig 2005; Park & Reuter-Lorenz 2009) and EEG data (Macpherson 2009; Friedman 1997) demonstrate that healthy aging results in increased reliance on frontal processes to compensate for lack of posterior activation. As older adults demonstrated an enhancement deficit in the P3b component and time window (300 to 500 msec after stimulus onset), frontally mediated compensation was assessed in this time window. Frontal electrode amplitude measures were submitted to an ANOVA with Task (attend, passive, and ignore) and Age (young, old) as factors. This analysis revealed a main effect of Age ($F(2, 76) = 15.60$, $p < 0.0001$, $\eta_p^2 = 0.12$), which demonstrated that younger adults exhibited more negative amplitudes compared to older adults. Notably, the amplitude of the identified component was negative for both older and younger adults, but less negative (i.e., more positive) in younger adults. No other main effects or interactions were observed for the frontal component amplitude.

4 DISCUSSION

The goal of this study was to examine whether predictive information enables older adults to appropriately suppress irrelevant information and exhibit working memory performance comparable to younger adults. It was hypothesized that this information would allow both older and younger participants to successfully attend to relevant information and ignore irrelevant information as they would know both the content of the stimuli and when the relevant stimuli would appear. Results revealed that when older adults were given these predictive cues, they responded with accuracies comparable to younger adults and, critically, exhibited comparable signals for neural suppression in association with ignoring irrelevant stimuli.

Despite comparable accuracies and suppression of neural activity to irrelevant information, older adults did exhibit longer response times that are not attributable to motoric slowing and displayed a slowed P1 as well as a reduced P3 amplitude enhancement to relevant information compared to younger adults. Importantly, older adults who exhibited the least P3 amplitude enhancement also exhibited the greatest declines in both working memory accuracy and response time. Together, these results suggest that predictive information alone is not sufficient for older adults to achieve working memory performance comparable to younger adults, although predictive information may facilitate processes that help maintain accuracy performance and neural suppression abilities.

Previous research indicated that older, compared to younger, adults experienced both lowered working memory performance and associated deficits in suppressing neutral activity in response to irrelevant stimuli. For example, when participants were provided predictive information regarding the content of the stimuli (remember faces, ignore scenes; remember scenes, ignore faces), older adults responded with lower accuracy compared to younger adults though they exhibited comparable response times (Gazzaley et al., 2008, 2005a). ERP data showed that older adults exhibited deficits in suppressing P1/P3 amplitude toward irrelevant stimuli and the timing of the N1 component did not differ when ignoring or passively viewing faces (suppression deficit) (Gazzaley et al., 2008), whereas blood oxygen level dependent (BOLD) activity from functional magnetic resonance imaging (fMRI) data has attributed these age-related suppression deficits to declines in stimulus-selective regions of visual cortex (Chadick et al., 2014; Gazzaley et al., 2005a). Similarly, when provided with predictive information regarding the timing of relevant and irrelevant stimuli, but not the content, older adults still exhibit P1 amplitude and N1 latency suppression deficits as well as lowered working memory accuracy (Zanto et al., 2010). Furthermore, when presented with only one relevant stimulus and no irrelevant stimuli, older adults exhibited diminished working memory accuracy, even when provided with predictive information regarding both the timing and the content of the stimulus (Bollinger et al., 2011). FMRI connectivity analysis demonstrated that these behavioral deficits in response to face stimuli are associated with decreased connectivity between the fronto-parietal attention network and the fusiform face area (Bollinger et al., 2011).

By contrast, the current results elucidate a more complex finding for age-related performance for settings when additional predictive cue information is provided (i.e., when relevant/irrelevant stimuli would appear and the content of these stimuli). Older adults maintained levels of accuracy comparable to younger adults when complex predictive cues were available. Yet, because older adults exhibited higher response times that cannot be attributed to motoric slowing as well as shifts in P3 signals associated with visual attention to relevant information, the current results may be indicative of an age-related shift from proactive to reactive cognitive states (Paxton et al., 2008), or a deficiency in expectation-related processes (Bollinger et al., 2011; Zanto et al., 2011).

Alternatively, due to the rapid shifting of attention to and away from relevant and irrelevant stimuli during the encoding period, it could be argued that the slower response times exhibited by older adults may be attributed to difficulty in attentional orienting. Indeed, older adults require more time to orient attention to a target (Amenedo et al., 2012), away from a target (Cona et al., 2013), and away from distractors (Cashdollar et al., 2013). Here, older adults exhibited a slowed P1 specifically to attended stimuli, which may represent declines in attentional orienting as early ERP components such as the P1 and N1 have been associated with attentional orienting processes (Nobre, 2001; Luck et al., 2000) and related to working memory performance for faces and scenes (Rutman et al., 2010). Thus, it is possible that deficient attentional orienting may have contributed to slowed response times in older adults, though a direct relationship between the P1 slowing and behavioral performance was not observed. Nonetheless, older adults retained the ability to suppress these early ERP components to irrelevant stimuli and this may have helped produce comparable accuracy performance between older and younger adults.

Older adults also often display a pattern of neural compensation through reduced posterior activity and greater anterior activity, which has been associated with retained task performance in aging (Davis et al., 2008; Cabeza 2002; Reuter-Lorenz & Lustig 2005; Park & Reuter-Lorenz 2009). Here, older adults displayed enhancement deficits in the posterior P3, and thus frontal activation during this time period was assessed as a potential marker for neural compensation. However, evidence of a frontal P3 component was lacking, as frontal activity was generally negative during this time period. Nonetheless, there was no Age ×

Task interaction and neither age group displayed frontal enhancement, indicating no evidence that frontal processes were recruited to compensate for age-related declines in posterior P3 enhancement. Additionally, Figure 6 shows frontal activity for both older and younger adults 300–500 msec post-stimulus onset, which highlight comparable frontal activity across groups, indicating that frontal compensation was unlikely.

The lack of age-related declines in early suppression abilities but a deficiency during later processing stages (i.e., during the P3) suggests predictive information may have served to help resolve an early-to-late shift in neural processing observed in older adults (Dew et al., 2012). Although older adults no longer exhibited a P3 enhancement deficit in a later time window, this later stage neural activity was not related to task performance. Regardless, age-related declines in P3 enhancement were associated with deficient working memory performance. These results are in line with research indicating the P3 amplitude plays a critical role in working memory tasks (Donchin and Coles, 1988) by updating the stored content (Polich and Kok, 1995) and as such, larger P3 amplitudes correspond to better memory performance (Fabiani et al., 1990; Noldy et al., 1990), specifically corresponding to faster response times (Perri et al., 2014). As older participants who exhibited high levels of P3 enhancement also demonstrated higher accuracies and faster response times, it seems that P3 enhancement was critical for proper working memory performance. Although the magnitude of P3 enhancement did not correlate with working memory performance, sub-group analysis of participants who exhibited large and small measures of P3 enhancement did show differential effects on working memory performance. Thus, declines in P3 enhancement are related to behavioral performance, but somewhat limited in predictive power due to the lack of a correlation. As the median split analysis does not account for the P3 enhancement variance as a continuous variable, the P3 enhancement deficit in aging is certainly not the sole source of performance declines. Yet, these results provide new and important information regarding the use of predictive information and how previously observed suppression deficits in aging (e.g., at the P1, N1, P3) (Gazzaley et al., 2005; Gazzaley et al., 2008; Zanto et al., 2010; Chadick et al., 2014) are not pervasive in cognitive aging. Whereas older adults were able to exhibit comparable suppression abilities and working memory accuracy with predictive cues, this additional information was not sufficient to overcome all age-related declines in working memory performance, such as updating working memory content.

CONCLUSION

Overall, the current results demonstrate that the use of predictive cues during a delayed working memory task reveal differential behavioral performance and neural processes between younger and older adults. Previous research has demonstrated working memory accuracy and neural suppression declines in aging when provided minimal cues, such as what type of stimulus to expect or when to expect relevant and irrelevant stimuli (Bollinger et al., 2011; Gazzaley et al., 2008, 2005a; Zanto et al., 2010). Here it was shown that when cues inform both what type of stimuli to expect and when to expect it, working memory accuracy and neural suppression is retained in aging. Rather, working memory response times and neural enhancement at later processing stages decline in older adults. Furthermore, older adults who exhibit the greatest declines in neural enhancement yield lowered working memory accuracy and slowed response times. This study demonstrates that predictive information regarding stimulus category and timing may help older adults with accuracy performance and neural suppression abilities, though these cues are still insufficient to result in equally matched response times and neural enhancement abilities between older and younger adults.

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Highlights

- Predictive cues enable comparable accuracy, not RT between older and younger groups
- No observed declines in P1/N1 amplitude/latency suppression to irrelevant stimuli
- Age-related decline in enhancing P3 to attended stimuli
- In aging, lower P3 enhancement tied to lower WM performance

Figure 1.

Experimental paradigm. Participants were instructed when to attend to specific types of stimuli, as indicated by the black bars beneath the relevant stimuli, each shown for 800 ms. After a 5 sec delay, a probe stimulus would appear for 1 sec which participants would identify as previously seen or not as quickly as possible without sacrificing accuracy.

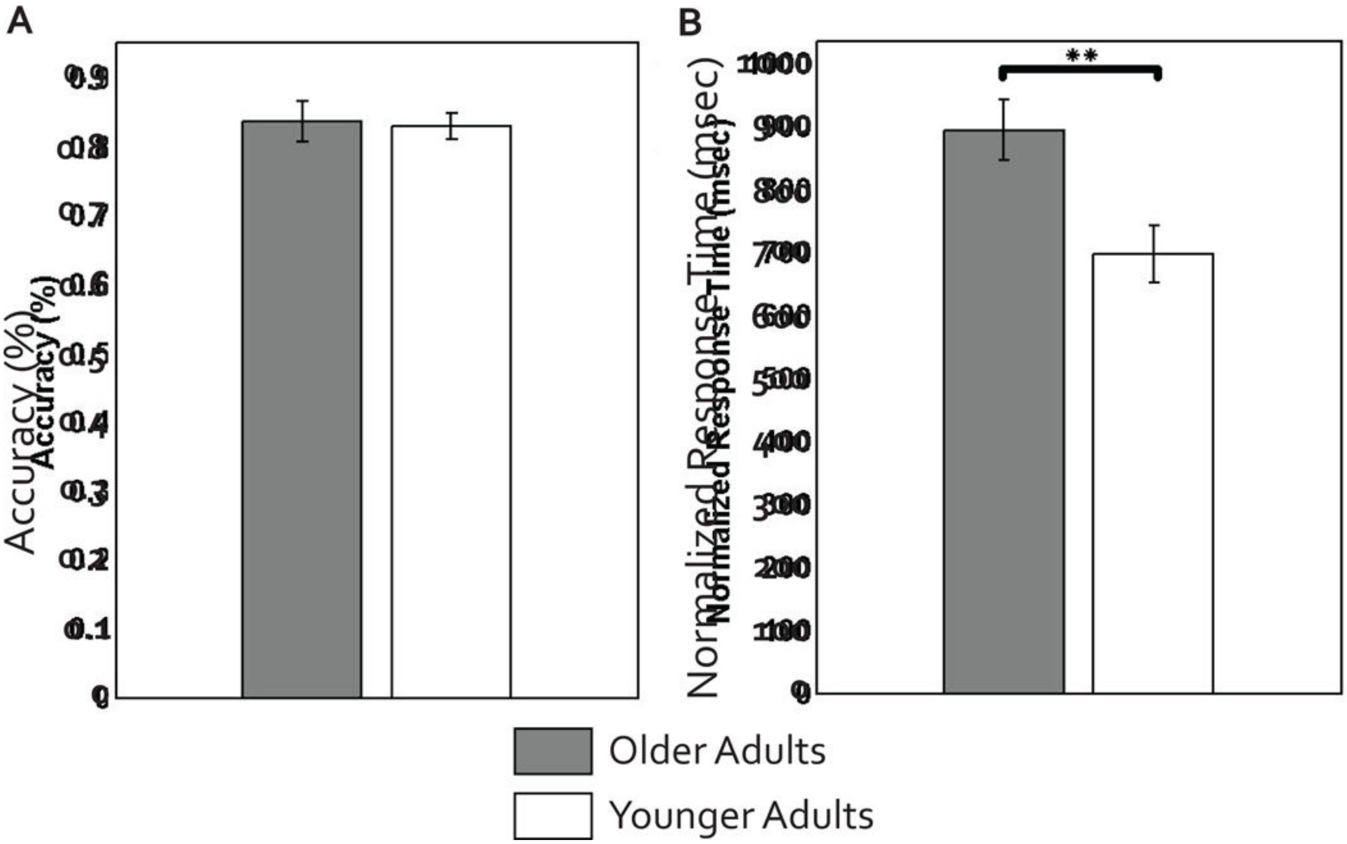

Figure 2.

Behavioral performance. (A) Average accuracy performance and (B) average normalized response time performance for younger and older adults.

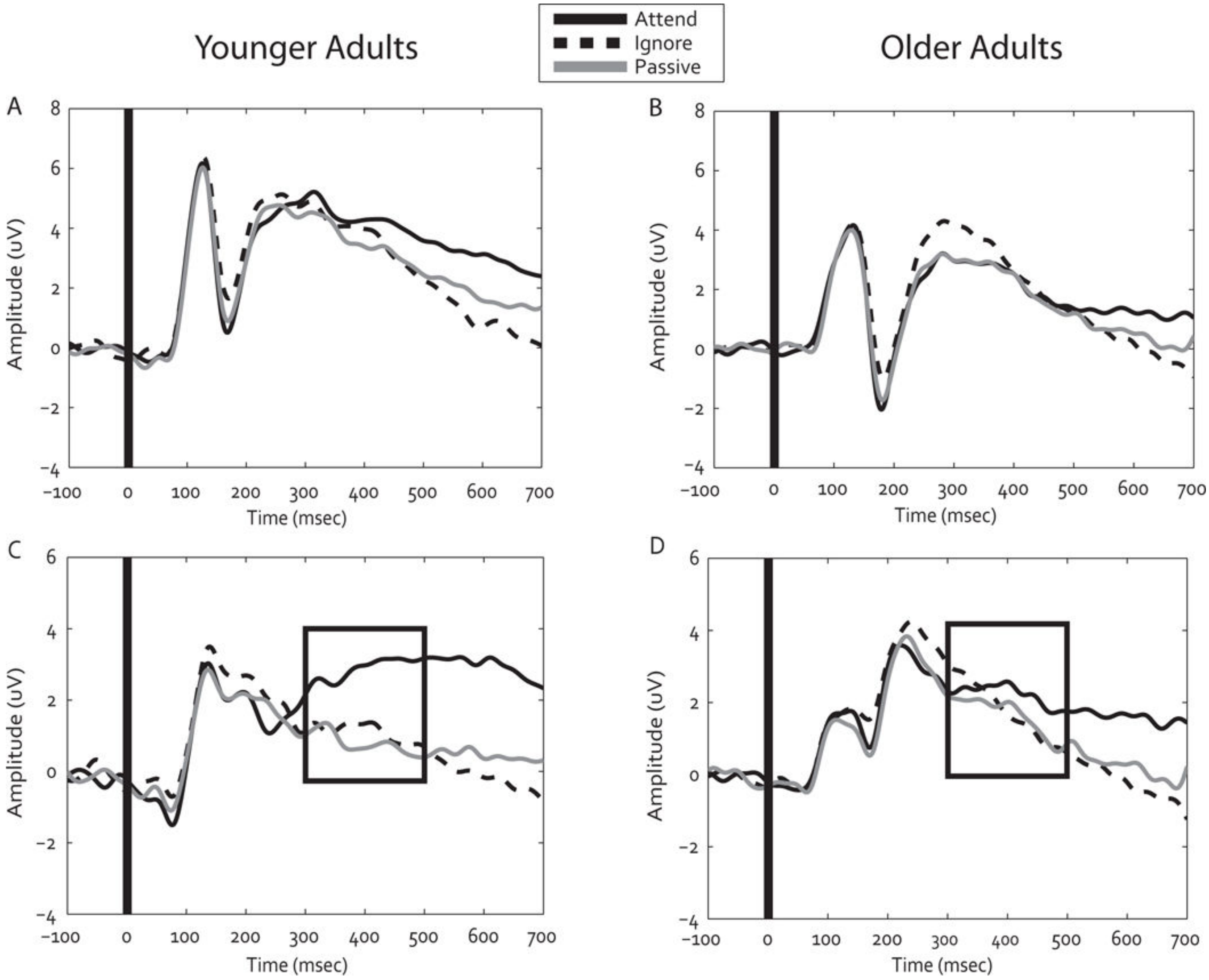

Figure 3.

Posterior neural performance. (A) P1 and N1 components of ERPs to face stimuli when attended, ignored, and passively viewed from younger adults and (B) from older adults. (C) P3 components of ERPs to face stimuli when attended, ignored, and passively viewed from younger adults and (D) from older adults.

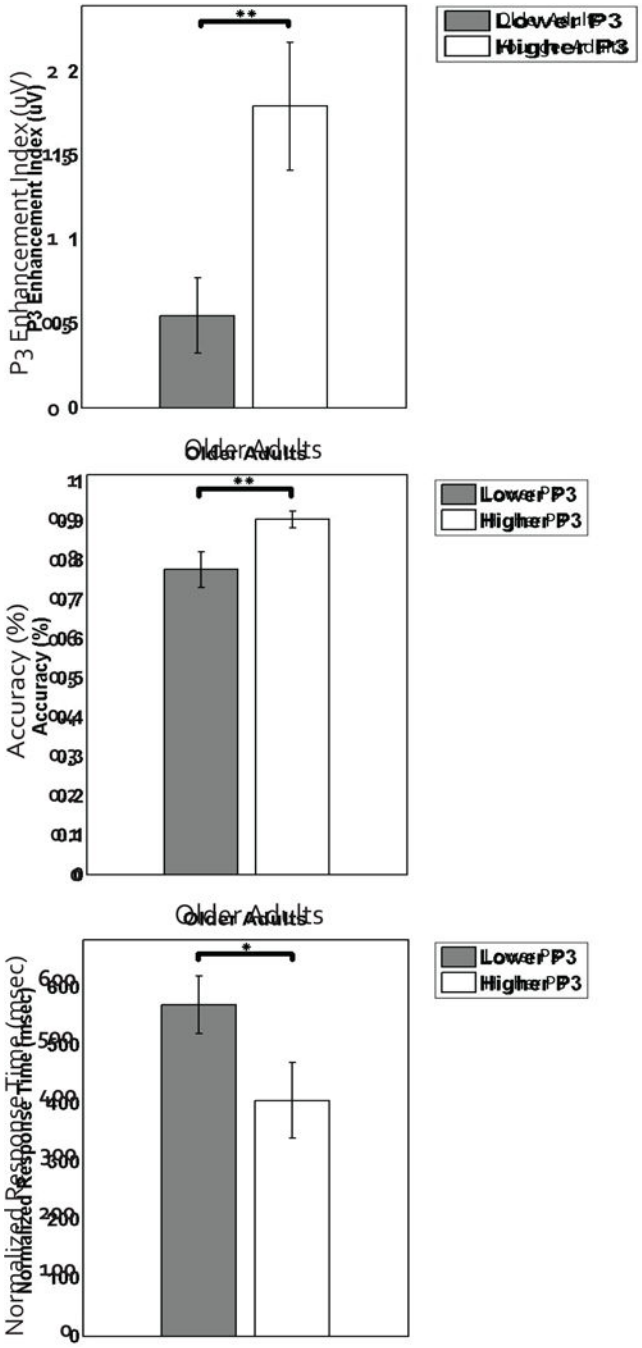

Figure 4.

Neural-behavioral relationship. (A) Difference in P3 enhancement modulation between younger and older adults. (B) Difference in accuracy performance and (C) normalized response time performance between older adults with high P3 enhancement and older adults with low P3 enhancement.

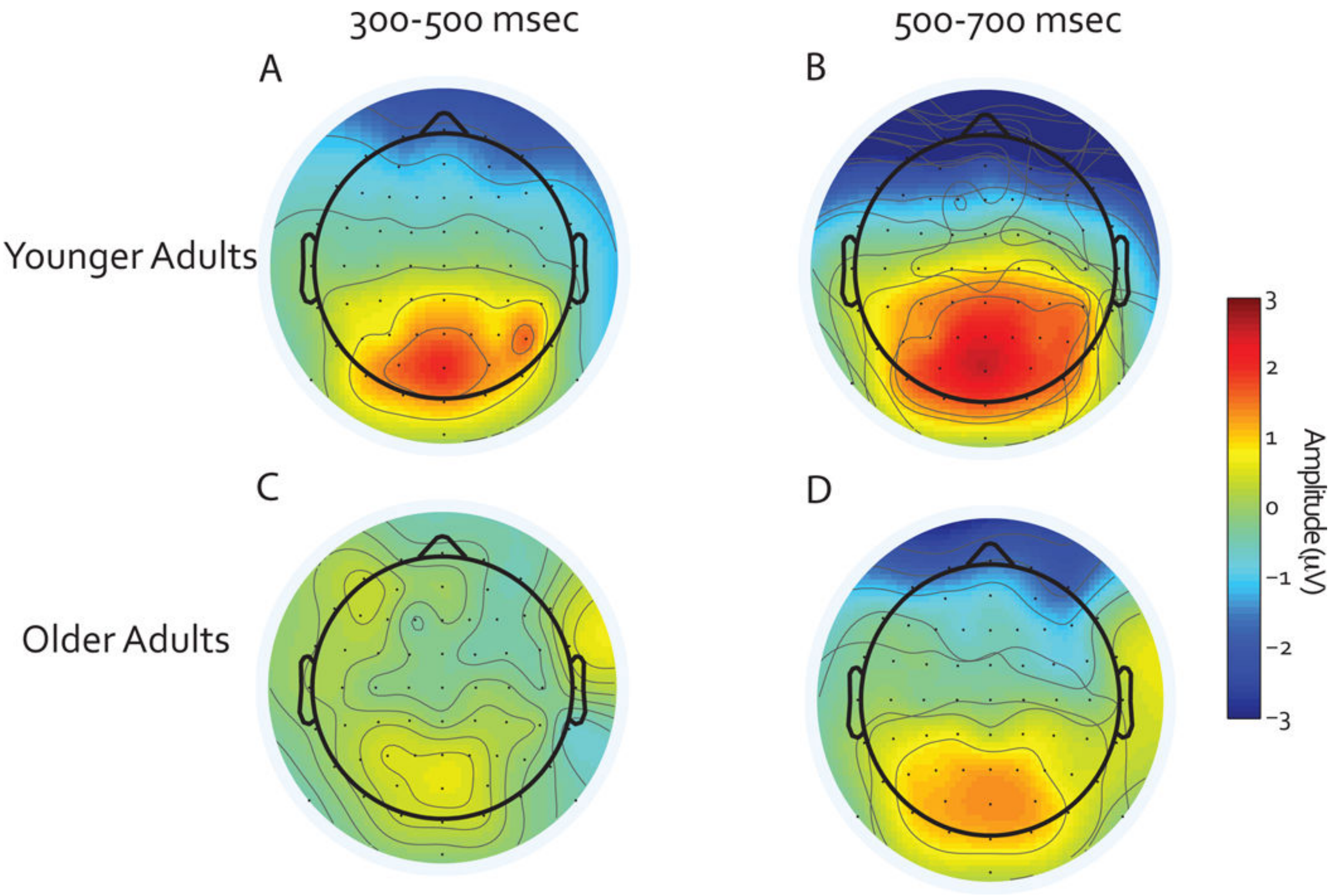

Figure 5.

Topographies. Whole brain enhancement activity (passive activity subtracted from attend activity) in response to face stimuli, for (A) younger adults, 300–500 msec post-stimulus onset, (B) younger adults, 500–700 msec post-stimulus onset, (C) older adults, 300–500 msec post-stimulus onset, and (D) older adults, 500–700 msec post-stimulus onset.

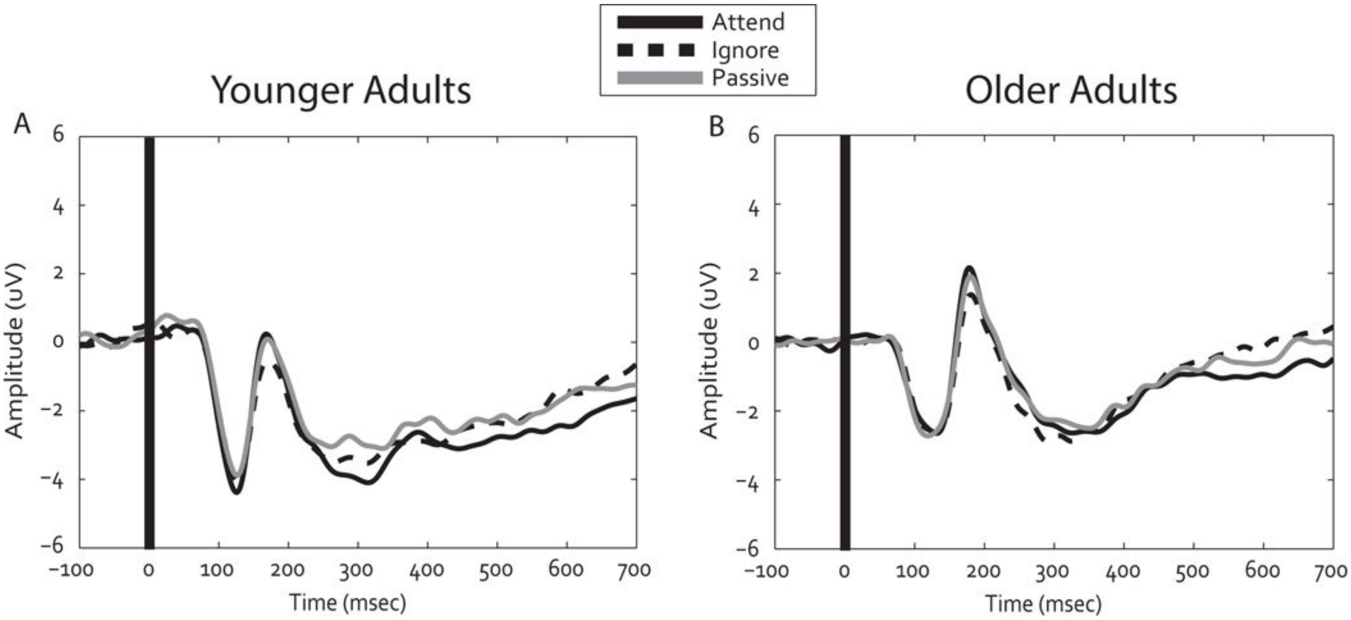

Figure 6.

Frontal neural performance. Frontal activity (300–500 msec post-stimulus onset) in response to face stimuli when attended, ignored, and passively viewed from (A) younger adults and from (B) older adults.

Table 1

Participant demographics. Values represent group mean values. Standard deviations are in parentheses.

	Younger (SD)	**Older (SD)**
N	20	20
Mean age (year)	24.4 (3.7)	72.4 (6.5)
Percent male	50%	45%
MMSE	n/a	29.5 (0.7)
GDS	n/a	2.5 (2.3)
Executive composite		
Stroop Interference		53.1 (12.7)
WAIS-R digit span (backward)		5.6 (1.2)
Memory composite		
CVLT: Trial 5 Recall		12.3 (2.1)
CVLT: short delay free recall		11.3 (3.2)
CVLT: short delay cued recall		11.7 (2.2)
CVLT: long delay free recall		10.9 (2.9)
CVLT: long delay cued recall		12.1 (2.7)
Memory for modified Rey recall		11.7 (4.8)
Memory for modified Rey recognition		1.4 (1.3)
Processing speed component		
Trailmaking test B		69.6 (16.7)
WAIS digit symbol test		52.3 (10.9)

SD, standard deviation.

MMSE, mini mental state examination (Folstein et al., 1975); GDS, geriatric depression scale.

WAIS, Weschler adult intelligence scale.

Table 2

Neural activity measures of interest. Standard error of mean in parentheses.

P1	**Younger Adults**		**Older Adults**	
	Amplitude (μV)	**Latency (msec)**	**Amplitude (μV)**	**Latency (msec)**
Attend	7.86 (0.44)	124.03 (1.50)	5.82 (0.49)	124.49 (1.86)
Ignore	7.92 (0.38)	126.85 (1.16)	5.93 (0.52)	123.78 (1.89)
Passive	6.84 (0.45)	122.19 (1.91)	5.06 (0.37)	116.32 (2.31)
N1	Younger Adults		Older Adults	
	Amplitude (μV)	Latency (msec)	Amplitude (μV)	Latency (msec)
Attend	−0.90 (0.62)	170.63 (1.70)	−3.74 (0.45)	180.06 (1.13)
Ignore	0.17 (0.56)	173.56 (1.94)	−3.13 (0.51)	181.00 (2.00)
Passive	−2.51 (0.44)	179.40 (1.77)	−4.12 (0.49)	181.90 (2.35)
P3 (300−500 msec)		Younger Adults	Older Adults	
		Amplitude (μV)	Amplitude (μV)	
Attend		2.86 (0.48)	2.23 (0.43)	
Ignore		1.10 (0.38)	1.77 (0.33)	
Passive		0.79 (0.48)	1.64 (0.35)	
P3 (500–700 msec)		Younger Adults	Older Adults	
		Amplitude (μV)	Amplitude (μV)	
Attend		2.96 (0.42)	1.60 (0.21)	
Ignore		−0.11 (0.43)	−0.21 (0.36)	
Passive		0.44 (0.35)	0.21 (0.19)	