Published in final edited form as:

Psychophysiology. 2014 July ; 51(7): 620–633. doi:10.1111/psyp.12206.

Investigating the age-related “anterior shift” in the scalp distribution of the P3b component using principal component analysis

Brittany R. Alperin^a, Katherine K. Mott^a, Dorene M. Rentz^a, Phillip J. Holcomb^b, and Kirk R. Daffner^a

^aCenter for Brain/Mind Medicine, Division of Cognitive and Behavioral Neurology, Department of Neurology, Brigham and Women's Hospital, Harvard Medical School, 221 Longwood Avenue, Boston, MA 02115, USA

^bDepartment of Psychology, Tufts University, 490 Boston Avenue, Medford, MA 02155, USA

Abstract

An age-related “anterior shift” in the distribution of the P3b is often reported. Temporospatial principal component analysis (PCA) was used to investigate the basis of this observation. ERPs were measured in young and old adults during a visual oddball task. PCA revealed two spatially distinct factors in both age groups, identified as the posterior P3b and anterior P3a. Young subjects generated a smaller P3a than P3b, while old subjects generated a P3a that did not differ in amplitude from their P3b. Rather than having a more anteriorly distributed P3b, old subjects produced a large, temporally overlapping P3a. The pattern of the age-related “anterior shift” in the P3 was similar for target and standard stimuli. The increase in the P3a in elderly adults may not represent a failure to habituate the novelty response, but may reflect greater reliance on executive control operations (P3a) to carry out the categorization/updating process (P3b).

Keywords

Cognition; EEG/ERP; Aging; PCA; Anterior Shift; P3

Introduction

The process of identifying and responding to target stimuli is critical to the execution of goal-directed behavior, and changes as individuals grow older. For example, several studies have shown that older adults utilize more anterior resources when detecting and responding to targets as compared to their younger counterparts (Braver et al., 2001; Fabiani, Friedman, & Cheng, 1998; Friedman, Kazmerski, & Cycowicz, 1998; West, Schwarb, & Johnson, 2010; West, 1996). Temporally precise event-related potentials (ERPs) are frequently used to understand the mechanisms underlying age-related differences in target processing (Fjell

& Walhovd, 2001; Friedman, 2003; Kok, 2000; Pfefferbaum, Ford, Wenegrat, Roth, & Kopell, 1984; Polich, 1996). There is evidence that the P3b component, which usually peaks between ~400–700 ms, reflects the categorization of an event according to task demands, the monitoring of decision making, or the updating of working memory once an event has been categorized (Daffner et al., 2011a; Donchin, 1981; Donchin & Coles, 1988; Knight & Scabini, 1998; Kok, 2001; Verleger, Jaskowski, & Wascher, 2005).

Anterior Shift Hypothesis

One finding in the ERP literature on cognitive aging is an “anterior shift” in the scalp distribution of the P3b to targets, which seems to “move” from a centro-posterior maximum in young adults to a uniformly distributed or more frontal maximum in older adults (Fabiani & Friedman, 1995; Fabiani et al., 1998; Friedman, Kazmerski, & Fabiani, 1997; Friedman, Simpson, & Hamberger, 1993; Li, Gratton, Fabiani, & Knight, 2013; West et al., 2010). Although there have been numerous aging studies using the P3b component as a dependent variable, many outstanding issues persist. It remains to be determined if young and elderly adults utilize the same basic neural network with differential activation of posterior and anterior nodes, or if elderly adults rely on a distinct set of frontal neural generators not utilized by young adults (Fabiani et al., 1998; Friedman et al., 1997).

Scalp distribution is one of the defining features of an ERP component and the P3b is in part characterized by its centro-posterior maximum. Because of this, some investigators have argued that the notion of an age-related anterior shift in the P3b is illogical (Donchin, Ritter, & McCallum, 1978; Spencer, Dien, & Donchin, 2001). Rather, the so-called anterior shift of the P3b is more likely the result of an anteriorly-distributed component that overlaps temporally with the P3b and indexes a different set of cognitive operations. A series of studies using principal component analysis (PCA) have found that young adults generate a large posterior component (consistent with the P3b) and a small anterior component (consistent with the P3a) in response to target events (Dien, 2012; Dien, Spencer, & Donchin, 2004; Spencer, Dien, & Donchin, 1999; Spencer et al., 2001). These investigators have not studied age-related changes in target processing using PCA.

An attractive hypothesis is that during the temporal interval of the P3, the increased frontal activity observed in older individuals is the reflection of a distinct anterior component such as the P3a.¹ The P3a is a frontally-distributed component, which in grand average ERPs temporally overlaps with the P3b, peaking between ~300–500 ms. The P3a has been interpreted as an index of the conscious aspect of the orienting response to novel/salient stimuli, or as a marker of an executive control process such as evaluating events or tasks to determine whether they merit additional processing or action (Barcelo, Escera, Corral, & Perianez, 2006; Barcelo, Perianez, & Knight, 2002; Daffner et al., 1998; Daffner et al., 2003; Dien et al., 2004; Friedman, Cycowicz, & Gaeta, 2001).

¹Of note in the literature, researchers differ in how they label the P3a component, which some call the novelty P3. The P3a was originally described as being elicited in response to infrequent stimuli during a two-stimulus oddball task or to identical stimuli when they were presented under an ignore condition (Squires, Squires, & Hillyard, 1975). The novelty P3 was initially characterized as being elicited in response to infrequent non-target events in a three-stimulus oddball task that involved the presentation of highly unusual stimuli (Courchesne, Hillyard, & Galambos, 1975). There is growing evidence to suggest that the P3a and the novelty P3 represent the same component (Simons, Graham, Miles, & Chen, 2001).

Principal Component Analysis (PCA)

Almost all studies investigating age-related changes in the P3b analyze their data through the traditional measurement of averaged ERP waveforms (Friedman et al., 1997; Kok, 2000; Polich, 1996). Though valuable, this method of analysis is not well suited for parsing spatially or temporally overlapping components such as the P3a and P3b. Although they overlap spatially and temporally, these two components are thought to reflect different cognitive operations (Polich, 2007; Soltani & Knight, 2000). The ability to distinguish one component from the other is critical for determining ways in which elderly adults may utilize cognitive operations that are different from their younger counterparts when carrying out a task. To address this issue, it is important to employ techniques that will aid in decomposing averaged waveforms. Thus, in addition to measuring averaged ERPs, we used temporospatial PCA, following a method developed by Dien (2012). PCA is a data driven method that decomposes an ERP waveform into its underlying components and is particularly useful in separating spatially and/or temporally overlapping components. Temporospatial PCA takes advantage of PCA's ability to parse components both temporally and spatially by breaking down each temporal principal component into a series of spatially distinct components. We used this method as a tool for helping to elucidate mechanisms underlying the age-associated anterior shift of the P3b.

Explanations for the Age-Related Anterior Shift

A common interpretation of the frontal shift of the P3b to target stimuli is that it represents the failure of older adults to habituate a novelty response to rare target events as they repeat, which manifests as larger anterior P3 activity (Fabiani et al., 1998; O'Connell et al., 2012; Richardson, Bucks, & Hogan, 2011). Furthermore, it has been proposed that the age-related failure to habituate may be due to the rapid decay of a mental template of target stimuli being held in working memory (Friedman et al., 1997). In the absence of a reliable representation of targets, the presentation of a target stimulus that deviates from the preceding series of repetitive standard stimuli leads to an orienting response. In contrast, young adults are able to quickly establish a strong mental representation of target stimuli, which facilitates the rapid habituation of the novelty response. This results in a much smaller anterior response to targets.

The age-related breakdown of habituation and the associated anterior shift of the P3b are often hypothesized to be due to dysfunction of the frontal lobes (Fabiani & Friedman, 1995; Fabiani et al., 1998; Friedman et al., 1993; Lorenzo-Lopez, Amenedo, Pazo-Alvarez, & Cadaveira, 2007; West et al., 2010). In support of this hypothesis, Fabiani et al. (1998) found that older subjects with a frontally oriented P3 performed worse on the Wisconsin Card Sorting Test, a putative measure of frontal lobe function, than subjects with a more parietally oriented P3. West et al. (2010) also provide supporting evidence for this hypothesis. They divided their older subjects by a median split using the composite score on three neuropsychological measures of executive function and found that only the bottom half of their elderly subjects generated a more frontally oriented P3 to targets. However, finding a difference in P3 scalp distribution among elderly adults who vary in executive capacity has not been universal (Daffner et al., 2006b; Fjell & Walhovd, 2005; Riis et al., 2008).

Motivation for the Current Study

Our approach to this issue has diverged from other investigations. In our studies we have selected subjects on the basis of their performance on neuropsychological tests relative to age-appropriate norms, rather than comparing the neuropsychological function of older subjects who differ in terms of their pattern of ERP response. This strategy is less dependent on the neuropsychological functioning of the particular subjects who happen to participate in an experiment. In a study using this approach, we found that cognitively high and cognitively average performers (based on a composite of six neuropsychological tests) did not differ in the scalp distribution of the P3 to target stimuli (Riis et al., 2008). Both groups generated a more anteriorly-distributed P3 response than their younger counterparts. West et al. (2010) has raised the issue of whether such findings differ from others in the literature because of our use of a general index of cognition rather than tests that emphasize executive function. To address this concern, we focused on a composite measure of executive function.

Our previous work also calls into question whether the age-related anterior shift in P3b response reflects changes specific to the processing of rare events like targets. In a subject-controlled visual novelty oddball task, we observed that older subjects also generated a more anteriorly-distributed P3 response to repetitive standard stimuli. Moreover, the magnitude of this shift was similar for targets and standards. When using techniques to account for the electrophysiological response to standard stimuli, there were no age-related differences in the scalp distribution of the P3 to targets (Riis et al., 2008). The current research allowed us to determine if this finding could be reproduced with a different set of subjects, using a different experimental paradigm. If this pattern were replicated, it would strongly support the notion that the anterior shift is not specific to the processing of rare events. Rather, this pattern may reflect salient age-related differences in the way in which all stimuli presented in a task are approached, which has been termed overall cognitive set or neural state in response to the demands of a task (Daffner et al., 2006b; Rugg & Morcom, 2005). It would also provide a challenge to the hypothesis that the anterior shift is due to a failure to habituate the neural response to rare events.

The primary purpose of this study was to investigate the age-related anterior shift of the P3b by using principal component analysis (PCA) to elucidate the mechanisms underlying this phenomenon. Specifically, the current study investigated several questions. Is the age-related anterior shift modulated by executive capacity? Is the anterior shift specific to the processing of rare events like targets or does it reflect a more general age-related change in the way in which the task is approached? And finally, does the anterior shift reflect activity of a single component that is more anterior in older subjects, or does it reflect the modulation of two separate components (one anterior and one posterior)? The results of these analyses would allow for inferences to be made about whether the age-related increase in neural activity of the anterior P3 reflects the modulation of activity within a common set of generators between young and elderly adults, or whether elderly adults recruit a distinct set of frontal generators. For example, do old adults depend on frontal generators not used by young adults and/or do they fail to utilize posterior processors used by young adults to carry out the task?

Methods

Participants

See Table 1 for subject characteristics, including demographic information, neuropsychological test performance, and estimated IQ for each age group. Subjects were recruited through community announcements in the Boston metropolitan area, including the Harvard Cooperative Study on Aging. All subjects underwent informed consent approved by the Partners Human Research Committee and a detailed screening evaluation that included a structured interview to obtain a medical, neurological, and psychiatric history; a formal neurological examination; the completion of a neuropsychological test battery; and questionnaires surveying mood and socioeconomic status.

To be included in this study, participants had to be between the ages of 18 and 32 or 65 and 80, be English-speaking, have 12 years of education, have a Mini Mental State Exam (MMSE) (Folstein, Folstein, & McHugh, 1975) score 26, and an estimated intelligence quotient (IQ) on the American National Adult Reading Test (AMNART) (Ryan & Paolo, 1992) 100. Subjects were excluded if they had a history of CNS diseases or major psychiatric disorders based on DSM-IV criteria (American Psychiatric Association, 1994), focal abnormalities on neurological examination consistent with a CNS lesion, a history of clinically significant medical diseases, corrected visual acuity worse than 20/40 (as tested using a Snellen wall chart), a history of clinically significant audiological disease, a Beck Depression Inventory (Beck & Steer, 1987) score 10 (for young subjects) or a Geriatric Depression Scale (Yesavage et al., 1982) score 10 (for old subjects), or were unable to distinguish between the color red and blue. Subjects were paid for their time.

To appropriately interpret age-related changes in neural activity, it is crucial to minimize differences between groups in cognitive abilities and task performance. If not, observed differences between groups may be due to factors other than age (Daffner et al., 2011b; Daselaar & Cabeza, 2005; Riis et al., 2008). Most investigations have not explicitly addressed this challenge. Due to strong support for the idea that selective attention reflects top-down control mechanisms (de Fockert, Rees, Frith, & Lavie, 2001; Gazzaley et al., 2008; Rissman, Gazzaley, & D'Esposito, 2009; Zanto, Rubens, Thangavel, & Gazzaley, 2011), we made an effort to match age groups in terms of executive capacity. One challenge to accomplishing this goal is the absence of a universally accepted operational definition of executive functions. We followed the suggestion of many investigators who emphasize processes that include working memory, initiation, monitoring, and inhibition, and advocate the use of at least several neuropsychological tests to assess this complex group of functions (Chan, Shum, Touloupoulou, & Chen, 2008; Delis, Kaplan, & Kramer, 2001; Spreen & Strauss, 1998). We selected tests that had well established norms across a wide range of ages. Tests of executive functions included: 1) Digit Span Backward subtest of the Wechsler Adult Intelligence Scale-IV (WAIS-IV) (Wechsler, 2008), measures maintenance and manipulation operations of working memory. 2) Controlled Oral Word Association Test (COWAT) (Ivnik, Malec, Smith, Tangalos, & Petersen, 1996) indexes initiation, self-generation, and monitoring. 3) WAIS-IV Letter-Number Sequencing assesses maintenance, monitoring, and manipulation. 4) WAIS-IV Digit-Symbol Coding assesses sustained

attention/persistence, cognitive speed and efficiency. 5) Trail-Making Test Parts A and B (Reitan & Wolfson, 1985) measure planning/sequencing, set shifting, and inhibition.

To qualify for the study, subjects had to have either high or average executive capacity, which was defined as the mean (composite) performance for the tests of executive function listed above. To meet the criteria for high capacity, subjects needed to perform in the top third (67th percentile) relative to age-appropriate norms. To meet the criteria for average capacity, subjects needed to perform in the middle third (33rd - 66th percentile) relative to age-appropriate norms. Consistent with suggestions in the aging literature, the groups were matched according to performance relative to age-appropriate norms (i.e., percentile scores) rather than absolute scores (Daffner et al., 2007; Daffner et al., 2006b; Daselaar & Cabeza, 2005; Riis et al., 2008). We did not include subjects who scored in the bottom third on neuropsychological tests to help exclude old subjects who may be suffering from mild cognitive impairment or the very early stages of a dementing illness.

Experimental Procedure

The experiment consisted of a color-selective attention task in which subjects were shown a series of letters presented in either the color red or the color blue and were asked to respond by button press to specific target letters. Task demands were made easier for old subjects to help minimize group differences in performance. The number of target letters chosen for each age group was based on pilot data: young subjects responded to 5 target letters and old subjects responded to 4 target letters. This was done to allow us to draw inferences about age-related differences in neural activity and not performance-related differences. Subjects were instructed to pay attention to letters appearing in the designated color while ignoring letters appearing in the other color, and to respond by button press to target letters appearing in the designated color only. Subjects were asked to respond as quickly and as accurately as possible to target letters. Practice trials preceded each set of experimental trials. The hand used for the target response and the attended color was counterbalanced across subjects.

See Figure 1 for a depiction of an experimental run. The task included 800 stimulus trials divided into 8 blocks. Stimuli appeared one at a time within a fixation box that remained on the screen at all times and subtended a visual angle of $\sim 3.5^\circ \times 3.5^\circ$ at the center of a high-resolution computer monitor. Half of the stimuli appeared in the color red and half in the color blue, in randomized order. Target stimuli (7.5% in attend color; 7.5% in ignore color) were 5 (for young) or 4 (for old) designated upper case letters. Standard stimuli (70% overall; 35% in each color) were any non-target upper case letters. Fillers accounted for the remainder of the stimuli presented. Visual stimuli subtended an angle of 2.5° along their longest dimension and were presented for 250 ms. The inter-stimulus interval (ISI) varied randomly between 815–1015 ms (mean ~ 915 ms). For analytic purposes, trials were further categorized in terms of whether the stimuli presented were in the attend or the ignore color. Of note, only stimuli in the attend color were analyzed in the current study.

ERP Recordings

An ActiveTwo electrode cap (Behavioral Brain Sciences Center, Birmingham, UK) was used to hold to the scalp a full array of 128 Ag-AgCl BioSemi (Amsterdam, The

Netherlands) “active” electrodes whose locations were based on a pre-configured montage. Electrodes were arranged in equidistant concentric circles from 10–20 system position Cz (see Alperin et al., 2013). In addition to the 128 electrodes on the scalp, 6 mini bio-potential electrodes were placed over the left and right mastoid, beneath each eye, and next to the outer canthi of the eyes to check for eye blinks and vertical and horizontal eye movements. EEG activity was digitized at a sampling rate of 512 Hz.

Data Analysis

Demographic variables and overall percentile performance on the neuropsychological tests for the groups were compared using one-way analysis of variance (ANOVA). Mean target accuracy and mean reaction time (RT) were measured. A response was considered a hit if it occurred between 200–1000 ms after stimulus presentation. Target stimuli correctly responded to (target hits) and stimuli incorrectly identified as targets (false alarms) were measured in order to determine an overall accuracy score (percent target hits – percent false alarms).

EEG data were analyzed using ERPLAB (www.erpinfo.org/erplab) and EEGLAB (Delorme & Makeig, 2004; <http://sccn.ucsd.edu/eeglab>) toolboxes that operate within the MATLAB framework. Raw EEG data were resampled to 256 Hz and referenced off-line to the algebraic average of the right and left mastoids. EEG signals were filtered using an IIR filter with a bandwidth of .03–40 Hz (12 dB/octave roll-off). Eye artifacts were removed through an independent component analysis. Individual bad channels were identified through visual inspection. Those that revealed a consistently different pattern of activity from all of the surrounding channels were corrected with the EEGLAB interpolation function. An average of 7.60 (4.23)% of channels were interpolated per subject. EEG epochs for the two stimulus types (target stimuli, standard stimuli) across two attention conditions (attend and ignore) were averaged separately. The sampling epoch for each trial lasted for 1200 ms, including a 200 ms pre-stimulus period that was used to baseline correct the ERP epochs. Trials were discarded from the analyses if they contained baseline drift or movement artifacts greater than 90 μ V. Only trials with correct responses were included in the analyses. Subjects were excluded from further analyses if their data were excessively noisy due to frequent contamination by alpha waves or motion artifacts.

For the average waveform ERP measure of the P3, the analysis focused on responses to target and standard stimuli under the attend condition. The latency was measured as the local positive peak and the size was measured as the mean amplitude between 400–700 ms at electrode sites FPz, Fz, Cz, and Pz for each stimulus type separately. Measurements were taken from midline electrode sites, because these have been the most common ones used to examine the P3 component (Fabiani et al., 1998; Friedman et al., 1997). Latency and amplitude were analyzed using ANOVA with electrode site as a within-subject variable, and age group and executive capacity group as the between-subject variables. The Greenhouse-Geisser correction was applied for all repeated measures with greater than 1 degree of freedom. Post-hoc comparisons were performed using a Bonferroni-Holm adjustment of p values for multiple comparisons (which has more statistical power than the traditional Bonferroni adjustment) (Holm, 1979). The number of post-hoc tests upon which adjustments

were made was determined based on the number of follow-up tests performed for a given effect or interaction.

Temporospatial Principal Component Analysis (PCA)

Following the recommendation of Dien (2012) a temporospatial PCA (temporal PCA followed by a spatial PCA) was conducted on averaged trials for each individual subject at all 134 electrode sites. ERPs to both target and standard stimuli under the attend and ignore conditions were included in the analysis. Utilizing the ERP PCA toolkit 2.38 (Dien, 2010), a Promax rotation was used and a covariance matrix and Kaiser normalization were applied to the data. Each dataset consisted of 307 time points between -200 and 1000 ms. A parallel test was used to restrict the number of factors generated for each PCA. Consistent with the literature, factors of interest were selected based on visual inspection of the timing and topography of the output (Dien, Spencer, & Donchin, 2003; Goldstein, Spencer, & Donchin, 2002; Spencer et al., 1999; Spencer et al., 2001). Any factors that accounted for > 0.5% of the total variance were considered for further analyses (Dien, 2012). Factor scores were submitted to statistical analysis using ANOVA.

Results

Participants

A total of 55 subjects participated in this study. There were 13 high and 13 average executive capacity young subjects, and 15 high and 14 average executive capacity old subjects. An additional 2 young-high capacity, 1 young-average capacity, 3 old-high capacity, and 2 old-average capacity subjects completed the experiment, but were excluded due to excessively noisy data.

A 2 age group (young and old) $\times$ 2 executive capacity group (high and average) ANOVA was run for each of the pertinent variables. For executive capacity (percentile based on age-appropriate norms) there was no effect of age group, $F(1,51) = .10, p = .76$, an effect of executive capacity group, $F(1,51) = 116.17, p < .001$, and no age group $\times$ executive capacity group interaction, $F(1,51) < .001, p = 1.00$. The effect of executive capacity group was due to high functioning subjects having a higher executive capacity percentile performance than average functioning subjects. For years of education, there was no effect of age group, $F(1,51) = 2.23, p = .14$, no effect of executive capacity group, $F(1,51) = 2.20, p = .14$, and no age group $\times$ executive capacity group interaction, $F(1,51) = .42, p = .52$. In terms of AMNART estimated IQ, there was no effect of age group $F(1,51) = .45, p = .51$, an effect of executive capacity group, $F(1,51) = 5.89, p = .02$, and no age group $\times$ executive capacity group interaction, $F(1,51) = .05, p = .82$. The executive capacity group effect was due to high capacity subjects having higher estimated IQs than average capacity subjects. For MMSE scores, there was an effect of age group, $F(1,51) = 6.11, p = .02$, no effect of executive capacity group, $F(1,51) = 1.29, p = .26$, and no interaction between age group and executive capacity group, $F(1,51) = .07, p = .79$. The age group effect resulted from young subjects having higher scores than old subjects.

Behavior

Target accuracy and mean reaction time (RT) data are presented in Table 2. Note that task demands were made easier for old subjects (4 target letters) than young subjects (5 target letters). For accuracy, a 2 age group $\times$ 2 executive capacity group ANOVA revealed no effect of age group, $F(1,51) = 2.08$, $p = .16$, an effect of executive capacity group, $F(1,51) = 7.20$, $p = .01$, and no age group $\times$ executive capacity group interaction, $F(1,51) = .55$, $p = .46$. The effect of executive capacity group was due to average capacity subjects performing worse on the task than high capacity subjects. In terms of RT, there was an effect of age group, $F(1,51) = 5.32$, $p = .03$, an effect of executive capacity group, $F(1,51) = 4.54$, $p = .04$, but no interaction between age group and executive capacity group, $F(1,51) = .09$, $p = .77$. The age group effect resulted from young subjects having a faster RT than old subjects. The effect of executive capacity group was due to average capacity subjects having a slower RT than high capacity subjects.

ERPs

The grand average ERP responses under the attend condition at midline sites FPz, Fz, Cz, and Pz, and topographic maps for young and old subjects to target and standard stimuli are presented in Figures 2 and 3. This paper focused on the impact of aging on the P3 component to targets and standards. Results are reported for target and standard stimuli separately in accordance with previous research. Preliminary analyses were run with executive capacity group as a between-subjects factor and it was discovered that none of the results were modulated by executive function (for traditional analysis: $ps = .24-.77$; for PCA: $ps = .20-.79$). Because of this, data for high and average subjects were collapsed for each age group. Main effects or interactions that did not include the factor of age group, as well as non-significant results, are not presented, unless of particular theoretical interest.

Traditional Analysis

Target Stimuli: An ANOVA for the P3 latency revealed an effect of electrode site, $F(3,159) = 15.59$, $p < .001$, $\epsilon = .73$, and no effect of age group, $F(1,53) = 2.34$, $p = .13$. The electrode effect was due to the latency peaking earlier at FPz and Fz than at Cz or Pz, $FPz = Fz < Cz = Pz$.

An ANOVA for the P3 amplitude revealed an effect of electrode site, $F(3,159) = 18.64$, $p < .001$, $\epsilon = .49$, an interaction between electrode site and age group, $F(3,159) = 20.99$, $p < .001$, and no effect of age group, $F(1,53) = .04$, $p = .84$. The electrode site effect was present because the amplitude increased from Fz to Pz with no difference in size between FPz and Fz ($FPz = Fz < Cz < Pz$). The electrode site $\times$ age group interaction was due to an electrode site effect for the young group, $F(3,75) = 44.66$, $p < .001$, $\epsilon = .46$, that was absent in the old group, $F(3,84) = 1.55$, $p = .23$, $\epsilon = .50$. For the young subjects, the amplitude of the P3 increased from Fz to Pz with no difference in size between FPz and Fz ($FPz = Fz < Cz < Pz$). For the old subjects, the size of the P3 did not differ across the four electrode sites ($FPz = Fz = Cz = Pz$). The electrode site $\times$ age group interaction can also be characterized by the group effect at FPz, $F(1,53) = 10.09$, $p = .002$ (young $<$ old), and Fz, $F(1,53) = 6.56$, $p = .01$ (young $<$ old), differing from the group effect at Cz, $F(1,53) = 5.56$, $p = .02$ (young $>$ old), and Pz, $F(1,53) = 8.96$, $p = .004$ (young $>$ old).

Standard Stimuli: An ANOVA for the P3 latency revealed an effect of electrode site, $F(3,159) = 5.75, p = .002, \epsilon = .79$, an effect of age group, $F(1,53) = 13.45, p = .001$, and an interaction between age group and electrode site, $F(3,159) = 3.24, p = .03$. The electrode effect was due to the latency peaking earlier at Pz than at FPz. The group effect was present because the P3 of the young group peaked later than that of the old group. The electrode $\times$ age group interaction was due to an electrode effect for the young group, $F(3,75) = 6.13, p = .002, \epsilon = .83$ (FPz = Fz = Cz > Pz), that was not significant in the old group, $F(3,84) = 1.58, p = .22, \epsilon = .69$.

An ANOVA for the P3 amplitude revealed an effect of electrode site, $F(3,159) = 14.26, p < .001, \epsilon = .53$, an effect of age group, $F(1,53) = 14.26, p < .001$, and an interaction between electrode site and age group, $F(3,159) = 14.67, p < .001$. The age group effect was due to the overall amplitude of the P3 being smaller for the young group than the old group. There was an electrode site effect because the amplitude increased from Fz to Pz with no difference in size between FPz and Fz (FPz = Fz < Cz < Pz). The electrode site $\times$ age group interaction was a result of there being an electrode site effect for the young group, $F(3,75) = 32.87, p < .001, \epsilon = .55$, that was absent in the old group, $F(3,84) = .70, p = .47, \epsilon = .51$. For the young subjects, P3 amplitude increased from Fz to Pz with no difference in size between FPz and Fz (FPz = Fz < Cz < Pz). For the old subjects, the size of the P3 did not differ across the four electrode sites (FPz = Fz = Cz = Pz). The electrode site $\times$ age group interaction can also be characterized by an effect of age group at FPz, $F(1,53) = 16.53, p < .001$ (young < old), Fz, $F(1,53) = 28.13, p < .001$ (young < old), and Cz, $F(1,53) = 9.98, p = .003$ (young < old), that was not significant at Pz, $F(1,53) = .12, p = .74$ (young = old).

Principal Component Analysis (PCA)—Figures 4 and 5 depict the topography of the factors of interest for both age groups in response to target and standard stimulus types respectively. A temporospatial PCA yielded 96 factor combinations (12 temporal factors, each with 8 spatial factors). A total of 63 of the factor combinations were not further analyzed because each accounted for < 0.5% of the total variance and were assumed to reflect noise. The initial temporal PCA yielded 12 temporal factors (TF) that accounted for 94.73% of the variance. We focused on factors during the temporal interval of the P3 (400–700 ms). There was one temporal factor that occurred within the appropriate temporal window and accounted for a substantial portion of the total variance: a positivity peaking at 503 ms (TF2) that accounted for 26.21% of the variance. A spatial PCA was performed on the temporal factor, and eight spatial factors (SF) were retained. Based on visual inspection of the timing and topography of the factors, two were of particular interest to the goals of this study. TF2SF1 accounted for 10.00% of the total variance, 38.15% of the variance within TF2, and had an anterior distribution consistent with the topography of a P3a (peaking at electrode FPz).² TF2SF2 accounted for 9.22% of the total variance, 35.18% of

²The P3a PCA factor peaks at FPz, which is more anterior than how the P3a component is commonly described in the literature. However, a majority of researchers examine the P3a using the traditional analysis of averaged waveforms rather than using PCA. Additionally, many studies measure the P3a at Fz and do not include FPz in their analyses (e.g., Fabiani et al., 1998; Friedman et al., 1997; Lorenzo-Lopez et al., 2007). In our analysis of the P3 using averaged waves, we did not find a difference in amplitude between FPz and Fz for either age group. Of note, in a study of young subjects using PCA, Dien (2012) also found a P3a factor peaking anterior to Fz. PCA was run on the data from young and old groups separately to confirm that the location of the P3a factor in the current study was not driven by the large anterior response in old subjects. The output revealed that both groups generated an anterior P3a factor peaking at electrode site FPz.

the variance within TF2, and had a centro-posterior distribution consistent with the topography of a P3b (peaking at electrode Pz).

Target Stimuli: A 2 factor (TF2SF1: P3a and TF2SF2: P3b) $\times$ 2 age group (young and old) ANOVA revealed an overall effect of factor, $F(1,53) = 6.96, p = .01$, an interaction between age group and factor, $F(1,53) = 23.75, p < .001$, and no effect of age group, $F(1,53) = .65, p = .43$. The factor effect was due to TF2SF2 being larger than TF2SF1. The age group $\times$ factor interaction was present because there was an effect of factor for the young group, $F(1,25) = 30.84, p < .001$ (TF2SF2 > TF2SF1), but not for the old group, $F(1,28) = 2.36, p = .14$ (TF2SF1 = TF2SF2). The age group $\times$ factor interaction can also be characterized by an age group effect for TF2SF1, $F(1,53) = 12.58, p = .001$ (young < old), that differed from the age group effect for TF2SF2, $F(1,53) = 5.44, p = .02$ (young > old).

Standard Stimuli: A 2 factor (TF2SF1: P3a and TF2SF2: P3b) $\times$ 2 age group (young and old) ANOVA revealed an effect of age group, $F(1,53) = 16.36, p < .001$, an effect of factor, $F(1,53) = 10.83, p = .002$, and an interaction between age group and factor, $F(1,53) = 20.78, p < .001$. The group effect was due to the young subjects generating a smaller response than old subjects.³ The factor effect resulted from TF2SF2 being larger than TF2SF1. The age group $\times$ factor interaction was due to an effect of factor for the young group, $F(1,25) = 28.67, p < .001$ (TF2SF2 > TF2SF1), but not for the old group, $F(1,28) = .86, p = .36$ (TF2SF1 = TF2SF2). The age group $\times$ factor interaction can also be characterized by an age group effect for TF2SF1, $F(1,53) = 28.06, p < .001$ (young < old), but no effect of age group for TF2SF2, $F(1,53) = 2.69, p = .11$ (young = old).⁴

Matching groups for non age-adjusted executive capacity scores: Because several reports in the literature have found that the scalp distribution of the P3 may be modulated by executive function (Fabiani et al., 1998; West et al., 2010) we explored this topic further. One concern with our methodology is that, although the young and old groups were matched for executive capacity based on age-appropriate norms, the raw scores of the young subjects were higher than the raw scores of the old subjects. We were interested in determining if a subset of young and old subjects, matched for executive capacity based on young adult norms, would show the same pattern as the entire group of young and old subjects matched for executive capacity based on age-appropriate norms. Young-average and old-high subjects were compared because the raw scores of young subjects with average capacity were similar to the raw scores of old subjects with high capacity.

When recoded according to young adult norms, the executive capacity composite percentile of old-high subjects did not differ from the executive capacity of young-average subjects, $F(1,26) = .14, p = .72$; young-average: $M = 54.04, SD = 11.46$; old-high: $M = 52.72, SD = 7.34$. A 2 factor (TF2SF1 and TF2SF2) $\times$ 2 age group (young-average and old-high)

³Interestingly, in response to standard stimuli, TF2SF1 was negative for young adults. The functional significance of this observation remains to be determined. Most relevant to the goals of this study was the finding that the difference in amplitude between the anterior and posterior factors was robust for both target and standard stimulus types.

⁴In order to verify that the results of the PCA were not being driven by latency differences between stimulus types, PCAs were conducted on target and standard stimuli separately. The pattern of results did not differ between the PCA run on each stimulus type alone and the PCA run on both stimulus types together.

ANOVA revealed an interaction between factor and age group for target stimuli, $F(1,26) = 6.60$, $p = .02$, and standard stimuli, $F(1,26) = 5.99$, $p = .02$. These interactions were present because the young-average subjects had a factor effect, targets: $F(1,12) = 10.77$, $p = .007$; standards: $F(1,12) = 7.77$, $p = .02$, whereas old-high subjects did not, targets: $F(1,14) = .51$, $p = .49$; standards: $F(1,14) = .20$, $p = .66$.⁵ In summary, the overall pattern of results with a subset of young and old subject groups matched for non age-adjusted norms was similar to the results with young and old subjects matched based on age-appropriate norms.

Discussion

The aim of the current study was to utilize PCA to better understand the age-related "anterior shift" of the P3b. The major findings of this study can be summarized as follows: 1) The average waveforms revealed a difference in P3 scalp distribution such that young subjects had a posterior maximum and old subjects showed no difference in P3 size across electrode sites. 2) Temporospacial PCA identified two distinct components that we have labeled as the P3a and P3b, both of which were present in old as well as young adults. 3) Young subjects generated a P3a that was smaller than their P3b. 4) Old subjects generated a P3a that did not differ in size from their P3b. 5) The pattern of the age-related anterior shift in scalp distribution was similar for rare target and frequent standard stimuli. 6) The age-related effects summarized above were not modulated by executive capacity.

Although the terminology used varies across the literature, there seems to be a consensus that elderly individuals exhibit an increase in frontal P3 activity in response to rare target events (Fabiani & Friedman, 1995; Fabiani et al., 1998; Friedman et al., 1997; Friedman et al., 1993; Li et al., 2013; West et al., 2010). A challenge in this area of research is the diverse nomenclature used to characterize the findings. For example, although Fabiani et al. (1998), Fabiani and Friedman (1995), and Friedman et al. (1993) frequently discuss an age-related anterior shift in the P3b in response to target stimuli, in a review of seven of their studies (Friedman et al., 1997), they conclude that older subjects generally have a "P3b" with two scalp foci, one anterior and one posterior. Studies that have carried out source analysis of surface ERPs or have used combined ERP and fMRI techniques provide additional support for the idea that older adults generate an anterior and posterior focus of P3 activity in response to targets (Anderer, Pascual-Marqui, Semlitsch, & Saletu, 1998; Frodl et al., 2000; O'Connell et al., 2012).

Traditional analysis of the ERP waveforms in the current study yielded results that are consistent with previous reports: older subjects demonstrated an anterior shift in the scalp

⁵This interaction can also be characterized by TF2SF1 being smaller for young-average subjects than old-high subjects (targets: $F(1,26) = 4.89$, $p = .04$; standards: $F(1,26) = 8.08$, $p = .009$), but TF2SF2 not differing between age groups (targets: $F(1,26) = .42$, $p = .52$; standards: $F(1,26) = 1.95$, $p = .17$). The finding that young-average subjects do not have a larger P3b factor than old-high subjects differs from the results of comparing all young to all old subjects. Collapsed across executive capacity, young subjects have a larger P3b than old subjects. In an exploratory analysis on the response to target stimuli, we found that the size of the P3b factor of old-high subjects did not reliably differ from old-average subjects ($p = .42$) or from the young subjects ($p = .17$) (it lies between all young and old-average subjects), while the amplitude of the P3b for old-average subjects was smaller than the young subjects ($p = .005$). This result suggests that old-high subjects may have a greater preservation of the functions indexed by the P3b. Due to the exploratory nature of these analyses and a lack of an overall interaction between age group and executive capacity group, no strong conclusion can be drawn. Future work is needed to explore the sources and implications of a potentially better preserved P3b in higher functioning elders.

distribution of the P3 to target stimuli (Fabiani & Friedman, 1995; Fabiani et al., 1998; Friedman et al., 1993; Li et al., 2013; West et al., 2010). However, analysis of average waveforms cannot inform us whether this finding is the reflection of spatially and temporally overlapping components. To investigate this question, the current study utilized PCA to decompose potentially overlapping components. The PCA supports the existence of two distinct components and not one widely distributed component. However, the power of PCA to decompose overlapping waveforms suggests that the pattern of results does not reflect the P3b component with a posterior and anterior focus, but rather that the posterior focus represents the P3b component and the anterior focus represents the P3a component.

Particularly relevant to the goals of this study, the PCA found that not only old, but also young subjects generated both a posterior and an anterior component in response to target stimuli. This observation may be obscured by analyses that rely solely on averaged waveforms, but has been reported in several studies of young adults using PCA (Dien, 2012; Dien et al., 2003; Dien et al., 2004; Spencer et al., 1999; Spencer et al., 2001). For example, using temporospatial PCA, Dien (2012) was able to spatially parse the P3 into an anterior P3a and a posterior P3b, both occurring within the same temporal factor.⁶ Our pattern of findings lends support to the hypothesis that young and elderly subjects may recruit a common set of nodes to carry out the task. However, there are age-related differences in the amount of resources allocated to operations indexed by each component. PCA itself does not locate underlying anatomical generators; however, a common assumption is that when surface potentials are similar between groups, the underlying neural generators are similar between groups (Urbach & Kutas, 2002).

The functional significance of the age-related difference in the size of the P3a

If we postulate that the larger anterior P3 response to target stimuli in older adults reflects an augmented P3a component, what is the functional significance of this age-related difference? Three non-mutually exclusive hypotheses are considered: 1) deficits in frontal-executive functions; 2) failure to habituate the anterior novelty response to rare targets; and 3) increased reliance on frontally-mediated cognitive control mechanisms.

Deficits in frontal-executive functions—The results of several studies provide support for the frontal-executive deficit hypothesis. Within the groups of older subjects investigated, those with evidence of reduced frontal lobe function (Fabiani et al., 1998), low executive capacity (West et al., 2010), or low task performance (Lorenzo-Lopez et al., 2007) generated a large anterior P3 to targets, while those who were high functioning did not (but generated a P3 with a posterior maximum). Our findings stand in contrast to these reports, as we found that old subjects with both average and high executive capacity generated an anterior P3 that was much larger than that of the young subjects. A potential concern with our analyses was our use of age-matched norms to determine whether subjects had average or high executive capacity since the raw scores of the young subjects were higher than the raw scores of our old subjects. To address this issue, we compared the ERPs of young-average subjects and

⁶With averaged waveforms, the anterior P3a often appears to peak earlier than the posterior P3b. In contrast, when using temporospatial PCA, Dien (2012) found that the P3a and P3b components are found within the same temporal factor.

old-high subjects since these two groups had comparable raw scores on the neuropsychological tests. We confirmed the finding that young subjects had a larger P3b than their P3a, while old subjects generated a P3a and P3b that did not differ in amplitude. This further suggested that the difference between groups is a reflection of the aging process rather than being due to differences in executive function.

The reasons contributing to why our results differ from those of several prior reports remain to be determined. Differences across studies include the criteria used to select subjects. Other studies have performed a median split on their sample of subjects according to task performance or neuropsychological test scores, whereas our subjects were explicitly chosen on the basis of their neuropsychological test performance. It seems unlikely that our results are simply a reflection of the particular subjects or particular paradigm used in this study, as the same kind of increase in anterior P3 activity was observed in different samples of average and high performing older subjects who have participated in other visual oddball or n-back tasks (Daffner et al., 2011a; Riis et al., 2008).

Failure to habituate the anterior novelty response to rare targets—Tightly linked to the frontal deficit hypothesis is the notion that the age-associated anterior shift in the P3b represents the failure of elderly subjects to appropriately habituate a novelty response to rare targets as they repeat (Friedman et al., 1997; Richardson et al., 2011; West et al., 2010). The identification by PCA of the anterior focus as the P3a component can be interpreted as strengthening this notion, since the P3a is often viewed as an index of the orienting response to novelty. The reduced capacity to habituate the novelty (P3a) response has been attributed to age-associated deficits in frontal lobe function that manifest as a decline in the ability to maintain a representation of rare target stimuli in working memory (Fabiani & Friedman, 1995; Fabiani et al., 1998; Friedman et al., 1997). However, a challenge to this hypothesis is our finding that the age-related increase in the P3a applies not only to targets, but also to standards. Observing salient age-related differences in the processing of standard stimuli (with elderly subjects generating a larger P3a) is not unique to the current investigation, but has been reported in prior studies (Daffner et al., 2005; Daffner et al., 2006b; Riis et al., 2008). It seems cumbersome to try to explain this phenomenon by attributing it to the failure to habituate a novelty response to repetitive standard events. A more straight-forward explanation is that it represents an important age-related change in the overall approach to the demands of a task, which affects the way in which resources are allocated to all stimulus types.

Increased reliance on frontally-mediated cognitive control mechanisms—In keeping with this idea, older subjects appear to approach this task and others by treating all stimuli as (relatively) attention-worthy. Within this framework, the age-associated enlargement of the P3a component may reflect an increased reliance on frontally-mediated control mechanisms. It has been suggested by several investigators that the P3a may be a manifestation of cognitive control activity (Barcelo et al., 2006; Barcelo et al., 2002; Daffner et al., 2000; Daffner et al., 2003; Goldstein et al., 2002). For example, based on our studies of focal lesion patients participating in a subject-controlled novelty oddball paradigm, we proposed that the P3a was a marker of frontal processes that determine the allocation of

attentional resources (Daffner et al., 2000; Daffner et al., 2003). In the current study, the age-associated augmentation of the anterior P3a may represent the marshalling of attentional/processing resources to stay on task and support the evaluative/categorization process being carried out in posterior regions of the brain.

This thesis is in line with the scaffolding theory of aging and cognition (STAC), which posits that age-related increases in frontal activity may reflect adaptive activation of complementary neural pathways to achieve cognitive goals in response to declining neural structure and function (Park & Reuter-Lorenz, 2009). Posteriorly-mediated operations indexed by the P3b appear to decline with age. Consistent with other studies (Anderer et al., 1998; Fabiani & Friedman, 1995; Fabiani et al., 1998; Li et al., 2013; O'Connell et al., 2012; Richardson et al., 2011), we found that younger subjects generated a larger P3b than older subjects. Although there is an ongoing debate in the literature, the P3b is often interpreted as a posteriorly-mediated index of the process of categorizing an event or updating working memory once an event has been categorized (Daffner et al., 2011a; Donchin, 1981; Donchin & Coles, 1988; Knight & Scabini, 1998; Kok, 2001). Consistent with STAC, the age-associated decrease in the functions indexed by the P3b may be partially compensated by frontal control mechanisms allowing for the adequate execution of the task.

At the level of demand elicited by the current study, young adults appear to be much less dependent on these frontal control mechanisms (as indexed by a much smaller P3a component). However, as shown in other research that employed a challenging n-back working memory task (Daffner et al., 2011a), young adults also demonstrate an augmentation of anterior P3 activity when the level of difficulty increases. This finding is consistent with the compensation-related utilization of neural circuits hypothesis (CRUNCH) (Reuter-Lorenz & Cappell, 2008). In accordance with CRUNCH, differences between young and elderly adults in the recruitment of operations indexed by the P3a may be a function of age-associated differences in processing capacity rather than the neural networks employed. Although recruiting more resources for low level task demands may result in elderly adults maintaining task performance, when faced with higher levels of difficulty they are at risk for running out of processing resources to adequately carry out the task.

Limitations

Several limitations of the current study deserve further comment. Because there was no novelty condition included in our analyses, we were unable to directly compare the P3a response to targets or standards to the novelty P3 generated in response to novel stimuli. However, the lack of a novelty condition does not seriously undermine our challenge to the hypothesis that the age-related increase in an anterior response is a reflection of an inability to inhibit a novelty response to rare target stimuli (Fabiani et al., 1998; O'Connell et al., 2012; Richardson et al., 2011). This thesis cannot adequately account for our observation that old subjects generated a P3a to repetitive standard stimuli in addition to rare targets. Another potential limitation is our method of matching young and old groups for task performance by making the task slightly easier for older subjects. Strong arguments have been made about the disadvantages of assessing differences in neural activity across groups

of subjects that vary in task performance (Daffner et al., 2006a; Rugg & Morcom, 2005). The concern is that this approach may not capture differences in neural activity due to age, but rather due to performance. We controlled for the potential confound of task performance by having task demands differ across age groups. One way to address the potential confounds of both task demand and task performance would be to include varying levels of task difficulty in future studies. This approach would provide the opportunity to examine if there were differences in neural activity between age groups matched for either task performance or task demand.

Additionally, a concern with PCA is that it may misallocate variance due to latency jitter (Mocks, 1986). There are several reasons why it is unlikely that latency jitter explains our results. First, as Dien (1998) points out, combining temporal with spatial PCA, as was done in this study, reduces the impact of latency (or spatial) jitter. Second, if latency jitter were driving our results, one would expect there to be two or more PCA factors within the temporal interval of interest. Only one temporal factor occurred within the temporal window of the P3 that accounted for a substantial portion of the total variance. Finally, the pattern of results did not differ between the PCA run on standard and target stimuli separately and the PCA run on both stimulus types together. This verifies that the results of the PCA were not being driven by latency differences between stimulus types.

Summary and future work

In summary, temporospatial PCA enabled us to disentangle the overlapping P3a and P3b components in average and high functioning young and old adults. Rather than old subjects generating an anterior shift in the distribution of the P3b, they generated a large P3a component that temporally overlapped with their P3b. Young subjects also generated a P3a to target stimuli, but on a much smaller scale. The PCA suggested that both young and elderly adults utilize a common set of nodes to carry out the task, but differ in the amount of resources allocated to the operations indexed by the P3a and P3b. We considered arguments interpreting the age-related increase in the P3a as a deficit in frontal lobe functioning associated with the failure to habituate the novelty response to targets. However, we favor the hypothesis that it may reflect the increased utilization of frontal executive functions to provide compensatory scaffolding to adequately carry out the task. In support of this notion, the age-related increase in the P3a was observed in response to both target and standard stimuli, suggesting that an increase in the allocation of anterior resources is not specific to the processing of rare events, but rather reflects a change in overall cognitive set or the way in which the task is approached.

Additional studies are needed utilizing PCA to investigate the age-related increase in frontal processing. Paradigms with additional conditions or stimulus types should be employed in order to clarify the functional significance of the age-related increase in the anterior component. It would be beneficial to confirm that the size of the P3a component in young adults increases under higher levels of task demand (Daffner et al., 2011a). Such a finding would support CRUNCH. The role executive function plays in carrying out the operations indexed by the P3a and P3b, particularly under higher task demands, remains to be determined. For example, when faced with a more difficult task, subjects with high, but not

average, executive capacity may have the resources necessary to successfully carry out the task. Additionally, our exploratory analyses suggested that the size of the P3b to targets may be better preserved in old subjects with high executive capacity (see footnote 3). Further research is needed to determine whether executive function modulates age-related changes in the P3b. To further investigate whether an increase in anterior activity may be due to an inability of older subjects to habituate a novelty response, future work should include examining changes in the P3a to target and standard stimuli across individual blocks or trials. Because PCA alone cannot identify the anatomical location of neural generators, additional work is needed using alternative methods, such as source localization, to further examine whether young and elderly adults are utilizing similar anatomical nodes to generate the P3a and P3b.

It is also important to pursue an understanding of how changes in earlier neurophysiological activity may differentially impact late processing and lead to a reduction in the amplitude of the P3b and an increase in the amplitude of the P3a. Work from our lab would point to the negative impact of slowed processing speed or suboptimal execution of earlier operations (like the mismatch N2) on subsequent operations, which then require the allocation of more resources to be carried out (Alperin et al., 2013; Daffner et al., 2011a; Riis et al., 2008).

Acknowledgments

This research was funded in part by NIA grant R01 AG017935 and by generous support from the Wimberly family, the Muss family, and the Mortimer/Grubman family. The authors would like to thank Christine Dunant for her excellent administrative assistance and Dr. Joseph Dien for his patient guidance in troubleshooting the PCA toolkit.

References

- Alperin BR, Haring AE, Zhuravleva TY, Holcomb PJ, Rentz DM, Daffner KR. The dissociation between early and late selection in older adults. *Journal of Cognitive Neuroscience*. 2013; 25(12): 2189–2206. [PubMed: 23915054]
- American Psychiatric Association. Diagnostic and statistical manual of mental disorders. 4th ed.. Washington, DC: American Psychological Association; 1994.
- Anderer P, Pascual-Marqui RD, Semlitsch HV, Saletu B. Differential effects of normal aging on sources of standard N1, target N1 and target P300 auditory event-related brain potentials revealed by low resolution electromagnetic tomography (LORETA). *Electroencephalography and Clinical Neurophysiology*. 1998; 108(2):160–174. [PubMed: 9566629]
- Barcelo F, Escera C, Corral MJ, Perianez JA. Task switching and novelty processing activate a common neural network for cognitive control. *Journal of Cognitive Neuroscience*. 2006; 18(10): 1734–1748. [PubMed: 17014377]
- Barcelo F, Perianez JA, Knight RT. Think differently: A brain orienting response to task novelty. *Neuroreport*. 2002; 13(15):1887–1892. [PubMed: 12395085]
- Beck, AT.; Steer, RA. Beck Depression Inventory: Manual. San Antonio, TX: The Psychological Corporation; 1987.
- Braver TS, Barch DM, Keys BA, Carter CS, Cohen JD, Kaye JA, Reed BR. Context processing in older adults: Evidence for a theory relating cognitive control to neurobiology in healthy aging. *Journal of Experimental Psychology: General*. 2001; 130(4):746–763. [PubMed: 11757878]
- Chan RC, Shum D, Touloupoulou T, Chen EY. Assessment of executive functions: Review of instruments and identification of critical issues. *Archives of Clinical Neuropsychology*. 2008; 23(2): 201–216. [PubMed: 18096360]

- Courchesne E, Hillyard SA, Galambos R. Stimulus novelty, task relevance and the visual evoked potential in man. *Electroencephalography and Clinical Neurophysiology*. 1975; 39:131–143. [PubMed: 50210]
- Daffner KR, Chong H, Riis J, Rentz DM, Wolk DA, Budson AE, Holcomb PJ. Cognitive status impacts age-related changes in attention to novel and target events in normal adults. *Neuropsychology*. 2007; 21(3):291–300. [PubMed: 17484592]
- Daffner KR, Chong H, Sun X, Tarbi EC, Riis JL, McGinnis SM, Holcomb PJ. Mechanisms underlying age- and performance-related differences in working memory. *Journal of Cognitive Neuroscience*. 2011a; 23(6):1298–1314. [PubMed: 20617886]
- Daffner KR, Mesulam MM, Scinto LF, Acar D, Calvo V, Faust R, Holcomb P. The central role of the prefrontal cortex in directing attention to novel events. *Brain*. 2000; 123(5):927–939. [PubMed: 10775538]
- Daffner KR, Mesulam MM, Scinto LF, Cohen LG, Kennedy BP, West WC, Holcomb PJ. Regulation of attention to novel stimuli by frontal lobes: An event-related potential study. *Neuroreport*. 1998; 9(5):787–791. [PubMed: 9579666]
- Daffner KR, Ryan KK, Williams DM, Budson AE, Rentz DM, Scinto LFM, Holcomb PJ. Age-related differences in novelty and target processing among cognitively high performing adults. *Neurobiology of Aging*. 2005; 26:1123–1295.
- Daffner KR, Ryan KK, Williams DM, Budson AE, Rentz DM, Wolk DA, Holcomb PJ. Age-related differences in attention to novelty among cognitively high performing adults. *Biological Psychology*. 2006a; 72(1):67–77. [PubMed: 16198046]
- Daffner KR, Ryan KK, Williams DM, Budson AE, Rentz DM, Wolk DA, Holcomb PJ. Increased responsiveness to novelty is associated with successful cognitive aging. *Journal of Cognitive Neuroscience*. 2006b; 18(10):1759–1773. [PubMed: 17014379]
- Daffner KR, Scinto LF, Weitzman AM, Faust R, Rentz DM, Budson AE, Holcomb PJ. Frontal and parietal components of a cerebral network mediating voluntary attention to novel events. *Journal of Cognitive Neuroscience*. 2003; 15(2):294–313. [PubMed: 12683359]
- Daffner KR, Sun X, Tarbi EC, Rentz DM, Holcomb PJ, Riis JL. Does compensatory neural activity survive old-old age? *Neuroimage*. 2011b; 54(1):427–438. [PubMed: 20696255]
- Daselaar, SM.; Cabeza, R. Age-related changes in hemispheric organization. In: Cabeza, R.; Nyberg, L.; Park, D., editors. *Cognitive neuroscience of aging*. New York: Oxford University Press; 2005. p. 325–353.
- de Fockert JW, Rees G, Frith CD, Lavie N. The role of working memory in visual selective attention. *Science*. 2001; 291(5509):1803–1806. [PubMed: 11230699]
- Delis, D.; Kaplan, E.; Kramer, J. *Delis Kaplan executive function system*. San Antonio, TX: Psychological Cooperation; 2001.
- 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(1):9–21. [PubMed: 15102499]
- Dien J. Evaluating two-step PCA of ERP data with geomin, infomax, oblimin, promax, and varimax rotations. *Psychophysiology*. 2010; 47(1):170–183. [PubMed: 19761521]
- Dien J. Applying principal components analysis to event-related potentials: A tutorial. *Developmental Neuropsychology*. 2012; 37(6):497–517. [PubMed: 22889342]
- Dien J, Spencer KM, Donchin E. Localization of the event-related potential novelty response as defined by principal components analysis. *Brain Research: Cognitive Brain Research*. 2003; 17(3): 637–650. [PubMed: 14561451]
- Dien J, Spencer KM, Donchin E. Parsing the late positive complex: Mental chronometry and the ERP components that inhabit the neighborhood of the P300. *Psychophysiology*. 2004; 41(5):665–678. [PubMed: 15318873]
- Donchin E. Presidential address, 1980. Surprise!...Surprise? *Psychophysiology*. 1981; 18(5):493–513. [PubMed: 7280146]
- Donchin E, Coles MGH. Is the P300 component a manifestation of context updating? *Behavioral and Brain Sciences*. 1988; 11:357–374.

- Donchin, E.; Ritter, W.; McCallum, WC. Cognitive psychophysiology: The endogenous components of the ERP. In: Callaway, E.; Tueting, P.; Kowlsow, S., editors. Event-related brain potentials in man. New York: Academic Press Inc.; 1978. p. 349–411.
- Fabiani M, Friedman D. Changes in brain activity patterns in aging: The novelty oddball. *Psychophysiology*. 1995; 32(6):579–594. [PubMed: 8524992]
- Fabiani M, Friedman D, Cheng JC. Individual differences in P3 scalp distribution in older adults, and their relationship to frontal lobe function. *Psychophysiology*. 1998; 35(6):698–708. [PubMed: 9844431]
- Fjell AM, Walhovd KB. P300 and neuropsychological tests as measures of aging: Scalp topography and cognitive changes. *Brain Topography*. 2001; 14(1):25–40. [PubMed: 11599530]
- Fjell AM, Walhovd KB. High versus average cognitive function: Implications for the age-sensitivity of P3. *Neurobiology of Aging*. 2005; 26(9):1305–1306.
- Folstein MF, Folstein SE, McHugh PR. "Mini-Mental State": A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research*. 1975; 12(3):189–198. [PubMed: 1202204]
- Friedman D. Cognition and aging: A highly selective overview of event-related potential (ERP) data. *Journal of Clinical and Experimental Neuropsychology*. 2003; 25(5):702–720. [PubMed: 12815507]
- Friedman D, Cycowicz YM, Gaeta H. The novelty P3: An event-related brain potential (ERP) sign of the brain's evaluation of novelty. *Neuroscience and Biobehavioral Reviews*. 2001; 25(4):355–373. [PubMed: 11445140]
- Friedman D, Kazmerski V, Fabiani M. An overview of age-related changes in the scalp distribution of P3b. *Electroencephalography and Clinical Neurophysiology*. 1997; 104(6):498–513. [PubMed: 9402892]
- Friedman D, Kazmerski VA, Cycowicz YM. Effects of aging on the novelty P3 during attend and ignore oddball tasks. *Psychophysiology*. 1998; 35:508–520. [PubMed: 9715095]
- Friedman D, Simpson G, Hamberger M. Age-related changes in scalp topography to novel and target stimuli. *Psychophysiology*. 1993; 30(4):383–396. [PubMed: 8327624]
- Frodl T, Juckel G, Gallinat J, Bottlender R, Riedel M, Preuss U, Hegerl U. Dipole localization of P300 and normal aging. *Brain Topography*. 2000; 13(1):3–9. [PubMed: 11073089]
- Gazzaley A, Clapp W, Kelley J, McEvoy K, Knight RT, D'Esposito M. Age-related top-down suppression deficit in the early stages of cortical visual memory processing. *Proceedings of the National Academy of Sciences of the United States of America*. 2008; 105(35):13122–13126. [PubMed: 18765818]
- Goldstein A, Spencer KM, Donchin E. The influence of stimulus deviance and novelty on the P300 and novelty P3. *Psychophysiology*. 2002; 39(6):781–790. [PubMed: 12462506]
- Holm S. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*. 1979; 6:65–70.
- Ivnik RJ, Malec JF, Smith GE, Tangalos EG, Petersen RC. Neuropsychological tests' norms above age 55: COWAT, BNT, MAE Token, WRAT-R Reading, AMNART, stroop, TMT, and JLO. *The Clinical Neuropsychologist*. 1996; 10(3):262–278.
- Knight RT, Scabini D. Anatomic bases of event-related potentials and their relationship to novelty detection in humans. *Journal of Clinical Neurology*. 1998; 15:3–13.
- Kok A. Age-related changes in involuntary and voluntary attention as reflected in components of the event-related potential (ERP). *Biological Psychology*. 2000; 54(1–3):107–143. [PubMed: 11035221]
- Kok A. On the utility of P3 amplitude as a measure of processing capacity. *Psychophysiology*. 2001; 38(3):557–577. [PubMed: 11352145]
- Li L, Gratton C, Fabiani M, Knight RT. Age-related frontoparietal changes during the control of bottom-up and top-down attention: An ERP study. *Neurobiology of Aging*. 2013; 34(2):477–488. [PubMed: 22459599]
- Lorenzo-Lopez L, Amenedo E, Pazo-Alvarez P, Cadaveira F. Visual target processing in high- and low-performing older subjects indexed by P3 component. *Neurophysiologie Clinique*. 2007; 37(2): 53–61. [PubMed: 17540288]

- Mocks J. The influence of latency jitter in principal component analysis of event-related potentials. *Psychophysiology*. 1986; 23(4):480–484. [PubMed: 3774929]
- O'Connell RG, Balsters JH, Kilcullen SM, Campbell W, Bokde AW, Lai R, Robertson IH. A simultaneous ERP/fMRI investigation of the P300 aging effect. *Neurobiology of Aging*. 2012; 33(10):2448–2461. [PubMed: 22277263]
- Park DC, Reuter-Lorenz P. The adaptive brain: Aging and neurocognitive scaffolding. *Annual Review of Psychology*. 2009; 60:173–196.
- Pfefferbaum A, Ford JM, Wenegrat BG, Roth WT, Kopell BS. Clinical application of the P3 component of event-related potentials. I. Normal aging. *Electroencephalography and Clinical Neurophysiology*. 1984; 59(2):85–103. [PubMed: 6200311]
- Polich J. Meta-analysis of P300 normative aging studies. *Psychophysiology*. 1996; 33(4):334–353. [PubMed: 8753933]
- Polich J. Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*. 2007; 118(10):2128–2148. [PubMed: 17573239]
- Reitan, R.; Wolfson, D. The Halstead-Reitan neuropsychological test battery: Theory and clinical interpretation. Tucson: Neuropsychology Press; 1985.
- Reuter-Lorenz PA, Cappell KA. Neurocognitive aging and the compensation hypothesis. *Current Directions in Psychological Science*. 2008; 17(3):177–182.
- Richardson C, Bucks RS, Hogan AM. Effects of aging on habituation to novelty: An ERP study. *International Journal of Psychophysiology*. 2011; 79(2):97–105. [PubMed: 20869996]
- Riis JL, Chong H, Ryan KK, Wolk DA, Rentz DM, Holcomb PJ, Daffner KR. Compensatory neural activity distinguishes different patterns of normal cognitive aging. *Neuroimage*. 2008; 39(1):441–454. [PubMed: 17931892]
- Rissman J, Gazzaley A, D'Esposito M. The effect of non-visual working memory load on top-down modulation of visual processing. *Neuropsychologia*. 2009; 47(7):1637–1646. [PubMed: 19397858]
- Rugg, MD.; Morcom, AM. The relationship between brain activity, cognitive performance, and aging. In: Cabeza, R.; Nyberg, L.; Park, D., editors. *Cognitive neuroscience of aging: Linking cognitive and cerebral aging*. Oxford University Press; 2005. p. 132–154.
- Ryan J, Paolo A. A screening procedure for estimating premorbid intelligence in the elderly. *Clinical Neuropsychologist*. 1992; 6(1):53–62.
- Simons RF, Graham FK, Miles MA, Chen X. On the relationship of P3a and the novelty-P3. *Biological Psychology*. 2001; 56:207–218. [PubMed: 11399351]
- Soltani M, Knight RT. Neural origins of the P300. *Critical Reviews in Neurobiology*. 2000; 14(3–4): 199–224. [PubMed: 12645958]
- Spencer KM, Dien J, Donchin E. A componential analysis of the ERP elicited by novel events using a dense electrode array. *Psychophysiology*. 1999; 36:409–414. [PubMed: 10352565]
- Spencer KM, Dien J, Donchin E. Spatiotemporal analysis of the late ERP responses to deviant stimuli. *Psychophysiology*. 2001; 38(2):343–358. [PubMed: 11347879]
- Spreen, O.; Strauss, E. A compendium of neuropsychological tests: Administration, norms, and commentary. 2nd ed.. New York: Oxford University Press; 1998.
- Squires NK, Squires KC, Hillyard SA. Two variables of long-latency positive waves evoked by unpredictable auditory stimuli in man. *Electroencephalography and Clinical Neurophysiology*. 1975; 38:387–401. [PubMed: 46819]
- Urbach TP, Kutas M. The intractability of scaling scalp distributions to infer neuroelectric sources. *Psychophysiology*. 2002; 39(6):791–808. [PubMed: 12462507]
- Verleger R, Jaskowski P, Wascher E. Evidence for an integrative role of P3b in linking reaction to preception. *Journal of Psychophysiology*. 2005; 19(3):165–181.
- Wechsler, D. Wechsler adult intelligence scale. 4th ed.. San Antonio, TX: Pearson; 2008.
- West R, Schwarb H, Johnson BN. The influence of age and individual differences in executive function on stimulus processing in the oddball task. *Cortex*. 2010; 46(4):550–563. [PubMed: 19720373]

- West RL. An application of prefrontal cortex function theory to cognitive aging. *Psychological Bulletin*. 1996; 120(2):272–292. [PubMed: 8831298]
- Yesavage JA, Brink TL, Rose TL, Lum O, Huang V, Adey M, Leirer VO. Development and validation of a geriatric depression screening scale: A preliminary report. *Journal of Psychiatric Research*. 1982; 17(1):37–49. [PubMed: 7183759]
- Zanto TP, Rubens MT, Thangavel A, Gazzaley A. Causal role of the prefrontal cortex in top-down modulation of visual processing and working memory. *Nature Neuroscience*. 2011; 14(5):656–661. [PubMed: 21441920]

Author Manuscript

Author Manuscript

Author Manuscript

Author Manuscript

Figure 1.
Illustration of an experimental run.

Target Stimuli

a) Grand Average Waves

b) Topographic Maps

Figure 2.

a) Illustration of the grand average ERP waveforms at midline electrode sites FPz, Fz, Cz, and Pz in response to target stimuli. b) Topographic maps of the mean amplitude between 400–700 ms in response to target stimuli.

Standard Stimuli

a) Grand Average Waves

b) Topographic Maps

Figure 3.

a) Illustration of the grand average ERP waveforms at midline electrode sites FPz, Fz, Cz, and Pz in response to standard stimuli. b) Topographic maps of the mean amplitude between 400–700 ms in response to standard stimuli. Note that the scale differs for target and standard stimulus types.

Target Stimuli

Figure 4. Waveforms and scalp topographies of PCA factors TF2SF1 (P3a) and TF2SF2 (P3b) in response to target stimuli.

Standard Stimuli

Figure 5. Waveforms and scalp topographies of PCA factors TF2SF1 (P3a) and TF2SF2 (P3b) in response to standard stimuli. Note that the scale differs for target and standard stimulus types.

Table 1

Subject Characteristics (Mean (SD))

	Young-High	Young-Average	Old-High	Old-Average
Number of subjects	13	13	15	14
Gender (male:female)	5:08	7:06	6:09	8:06
Age (years) ^a	22.54 (1.66)	22.62 (2.72)	73.93 (3.67)	71.64 (3.79)
Executive Capacity (%ile) ^b	80.71 (8.20)	54.05 (11.46)	81.50 (7.54)	54.81 (9.20)
Years of Education	15.88 (1.58)	14.42 (1.13)	16.47 (3.72)	15.89 (2.63)
AMNART (estimated IQ) ^c	119.15 (4.63)	114.31 (7.67)	121.13 (8.53)	115.29 (10.41)
MMSE ^d	29.92 (.28)	29.77 (.44)	29.53 (.74)	29.29 (.91)

^a effect of age group, $p < .001$ (young < old)

^b effect of executive capacity group, $p < .001$ (average < high)

^c effect of executive capacity group, $p = .01$ (average < high)

^d effect of age group, $p = .02$ (young > old)

Executive Capacity = Average (composite) percentile performance on the following tests: Digit Span Backward, Controlled Oral Word Association Test, Letter-Number Sequencing, Trail-Making Test Parts A and B, and Digit-Symbol Coding.

AMNART = American National Adult Reading Test

MMSE = Mini Mental State Exam

Table 2

Accuracy and Mean RT (Mean (SD))

	Young-High	Young-Average	Old-High	Old-Average
Accuracy (%) ^a	91.73 (7.32)	85.03 (6.22)	93.09 (4.97)	89.30 (9.45)
Mean RT (ms) ^{b, c}	592 (40)	628 (57)	631 (59)	658 (59)

^a effect of executive capacity group, $p = .01$ (high > average)^b effect of executive capacity group, $p = .03$ (high < average)^c effect of age group, $p = .04$ (young < old)

Accuracy = % target hits - % false alarms