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Investigating age-related changes in anterior and posterior neural activity throughout the information processing stream

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Abstract

Event-related potential (ERP) and other functional imaging studies often demonstrate age-related increases in anterior neural activity and decreases in posterior activity while subjects carry out task demands. It remains unclear whether this “anterior shift” is limited to late cognitive operations like those indexed by the P3 component, or is evident during other stages of information processing. The temporal resolution of ERPs provided an opportunity to address this issue. Temporospatial principal component analysis (PCA) was used to identify underlying components that may be obscured by overlapping ERP waveforms. ERPs were measured during a visual oddball task in 26 young, 26 middle-aged, and 29 old subjects who were well-matched for IQ, executive function, education, and task performance. PCA identified six anterior factors peaking between ~140 ms and 810 ms, and four posterior factors peaking between ~300 ms and 810 ms. There was an age-related increase in the amplitude of anterior factors between ~200 and 500 ms, and an age-associated decrease in amplitude of posterior factors after ~ 500 ms. The increase in anterior processing began as early as middle-age, was sustained throughout old age, and appeared to be linear in nature. These results suggest that age-associated increases in anterior activity occur after early sensory processing has taken place, and are most prominent during a period in which attention is being marshaled to evaluate a stimulus. In contrast, age-related decreases in posterior activity manifest during operations involved in stimulus categorization, post-decision monitoring, and preparation for an upcoming event.

Keywords

ERP; Principal component analysis; Aging; Anterior; Posterior

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.bandc.2015.08.001>.

1. Introduction

Functional neuroimaging studies commonly report an age-associated increase in anterior neural activity when subjects carry out a task (Davis, Dennis, Daselaar, Fleck, & Cabeza, 2008; Grady, 2000; Reuter-Lorenz & Sylvester, 2005). The current temporal resolution of fMRI limits the ability to determine when along the information processing stream these age-related differences take place. However, this issue can be effectively addressed through the investigation of event related potentials (ERPs). Most ERP studies have focused on the age-related augmentation in frontal activity during relatively late processing, as indexed by the anterior P3 (P3a) component (Alperin, Mott, Rentz, Holcomb, & Daffner, 2014b; Fabiani, Friedman, & Cheng, 1998; Friedman, Kazmerski, & Fabiani, 1997; West, Schwarb, & Johnson, 2010). An outstanding question involves the extent to which the age-associated increase in anterior activity is limited to late cognitive operations or is present throughout the information processing stream. It is also unclear whether the age-related augmentation in anterior activity reflects a maladaptive or compensatory response (Friedman et al., 1997; Reuter-Lorenz et al., 2000; Riis et al., 2008; West et al., 2010).

In addition to the common finding of an age-related increase in anterior activity, ERP researchers often report an age-related decrease in posterior activity (Ally, Simons, McKeever, Peers, & Budson, 2008; Anderer, Semlitsch, & Saletu, 1996; Fjell & Walhovd, 2001; Friedman et al., 1997; Wolk et al., 2009). For example, in ERP research, older individuals frequently exhibit a smaller posterior P3b (Anderer et al., 1996; Fjell & Walhovd, 2001; Friedman et al., 1997) or late positive component (LPC) (Ally et al., 2008; Wolk et al., 2009) than younger adults. It remains to be determined whether age-related reductions in posterior activity are limited to late cognitive operations or occur throughout the processing stream.

Most ERP studies examine age-related differences through traditional analyses of averaged waveforms. Although valuable, this form of analysis does not allow one to disentangle temporally and/or spatially overlapping components. In the current study, we used temporospatial PCA, following a method developed by Dien (2010a). PCA is a data driven method that decomposes ERP waveforms into their underlying components and is particularly useful in separating spatially and/or temporally overlapping components. Temporospatial PCA takes advantage of this method's ability to parse components both temporally and spatially by breaking down each temporal principal component into a series of spatially distinct components. In our previous work using PCA, we found that during the temporal interval of the P3a (400–600 ms), older individuals generated a larger response that was interpreted as reflecting increased utilization of anterior neural resources (Alperin, Mott, Holcomb, & Daffner, 2014a; Alperin et al., 2014b). Here, our approach using PCA was broadened to identify distinct anterior and posterior components in addition to the P3, and determine whether they exhibit age-associated differences in amplitude.

Many previous studies, including our own (Alperin et al., 2014a, 2014b), have investigated age-related differences and limited their comparison to young (college-aged) vs. old (~70 years) adults (Fabiani et al., 1998; Lorenzo-Lopez, Amenedo, Pazo-Alvarez, & Cadaveira, 2007; West et al., 2010). This approach, however, does not allow for the examination of

changes that may take place over the adult life span. In the current study, we addressed this limitation by including young, middle-aged, and old subjects ranging in age from 19 to 79 years old. This age-range allowed us to determine whether the most prominent changes emerge during old age (>65 years old) or begin during middle age, and whether the age-related differences are linear in nature. Based on prior work (Daffner, Alperin, Mott, Tusch, & Holcomb, 2015; Riis et al., 2009), we expected to find age-related increases in anterior activity beginning around the temporal interval of the anterior P2 component (~150–200 ms) and age-related decreases in posterior activity beginning around the temporal interval of the P3b (~400–600 ms). Moreover, we anticipated that changes would be observed by middle age (Riis et al., 2008).

2. Methods

2.1. 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 (young), 40 and 60 (middle-aged), or 65 and 79 (old), 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 and middle-aged subjects) or a Geriatric Depression Scale (Yesavage et al., 1983) 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.

Executive capacity was defined as the composite percentile performance (relative to age-matched norms) on the six tests of executive function listed above. To meet criteria for the study, subjects needed to perform in the top two thirds ($\geq$ 33rd percentile) relative to age-appropriate norms. 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.

2.2. Experimental procedure

Fig. 1 depicts an experimental run. 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 and middle-aged 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.

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 and middle-aged) or 4 (for old) designated upper case letters. Standard stimuli (70% overall; 35% in each color) were any non-target upper case letters. The target letters were KQXA (and T for young and middle-aged) or WGZE (and V for young and middle-aged). Half the subjects were presented one version and half the other, the order of which was counterbalanced. Standard

letters were any of the remaining letters. Unique line drawings (e.g., geometric shapes, impossible objects) accounted for the remaining 15% of the stimuli presented (7.5% in each color) and were not analyzed in this study. 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 and 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.

2.3. 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 to 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.

2.4. 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 and 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 (Lopez-Calderon & Luck, 2014; 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 bandpass 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. Channels that revealed a consistently different pattern of activity from all of the surrounding channels were corrected with the EEGLAB interpolation function. 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 for baseline correction. Trials were discarded from the analyses if they contained baseline drift or movement artifacts greater than 90 µV. 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.

2.5. Average wave forms

Time course analysis was performed on the average waveforms in response to target stimuli under the attend condition at anterior and posterior sites centered around Fz and Pz respectively (see Fig. 2). Repeated measures ANOVAs were run with the 16 time intervals (50 ms epochs between 0 and 800 ms) as within-subjects variables and age group as the between-subjects variable for anterior and posterior sites separately. If a reliable interaction between time interval and age was found, post-hoc one-way ANOVAs were run for each time interval, with age group as the between-subject variable. The Holm–Bonferroni method was used to control for multiple comparisons.

2.6. 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.¹ 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, 2010b), 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, Dien, & Donchin, 1999, 2001). Any factors that accounted for >2% of the total variance were considered for further analyses (Dien, 2012). Factor scores for each PCA factor were submitted to statistical analysis using repeated measures ANOVA with factor score as the within subject variable and age group as the between subject variable. ANOVAs were run separately for anterior and posterior factors. If a reliable interaction between PCA factor and age group was identified, post hoc one-way ANOVAs were run for each PCA factor, with age group as the between-subject variable. The Holm–Bonferroni method was used to control for multiple comparisons.

3. Results

3.1. Participants

A total of 81 subjects participated in the study. There were 26 young, 26 middle-aged, and 29 old adults. An additional 3 young, 6 middle-aged, and 5 old subjects completed the experiment, but were excluded due to excessively noisy data. See Table 1 for subject demographic information. One way ANOVAs were run for each of the pertinent demographic variables, with age group as the between subject variable. There was no effect of age group for executive capacity, $F(2,78) = .10$, $p = .91$, $\eta^2 = .002$, years of education, $F(2,78) = 2.44$, $p = .10$, $\eta^2 = .06$, or estimated IQ, $F(2,78) = .36$, $p = .70$, $\eta^2 = .01$. There was an effect of age group for scores on the Mini-Mental State Examination (MMSE), $F(2,78) = 4.38$, $p = .02$, $\eta^2 = .11$, such that the young subjects had slightly higher scores than the middle-aged and older subjects.

¹Temporospatial PCA was repeated on the data for each age group separately. These PCAs revealed that each age group had the same component structure that was identified when all of the groups were combined in one analysis.

3.2. Behavior

Target accuracy and mean RT data are presented in Table 1. There was no effect of age group for accuracy, $F(2,77) = 1.20, p = .03, \eta^2 = .31$, or RT, $F(2,77) = 1.90, p = .16, \eta^2 = .05$. Note that task demands were made easier for old subjects (4 target letters) than young and middle-aged subjects (5 target letters).

3.3. ERPs

3.3.1. Average waveforms—Fig. 2 depicts the grand average waveforms for target stimuli in the attend condition for each age group at anterior (Fz and 9 surrounding electrodes) and posterior sites (Pz and 9 surrounding electrodes). Inspection of the waveforms suggests that, at anterior sites, middle-aged and old subjects generated larger responses than young subjects between ~150 and 600 ms, whereas at posterior sites, they generated smaller responses between ~400 ms and 800 ms. Repeated measures ANOVA confirmed that there was a significant difference in the age-related pattern across time intervals (time interval $\times$ age group interaction) at both the anterior $F(30,1170) = 2.84, p = .01, \eta^2 = .07$, and posterior, $F(30,1170) = 4.22, p < .001, \eta^2 = .10$, sites. To understand this interaction, the mean amplitude for 50 ms epochs from 0 to 800 ms were analyzed at anterior and posterior sites for age-related differences, the results of which are provided in Table 2. The time course analysis demonstrated that, after controlling for multiple comparisons, between 150 and 400 ms and 500–550 ms there was an age-related increase in anterior potentials (with marginal effects for the 400–450, 450–500, 550–600 ms intervals), and between 550 and 800 ms there was an age-related decrease in posterior potentials (with marginal effects for the 400–450, 450–500, and 500–550 ms intervals).

3.3.2. Principal component analysis (PCA)—A temporospatial PCA yielded 117 factor combinations (13 temporal factors, each with 9 spatial factors). Ninety-seven of the factor combinations were not further analyzed because each accounted for <2% of the total variance. The initial temporal PCA yielded 13 temporal factors (TF) that accounted for 94.84% of the variance. A spatial PCA was performed on each of the 13 TFs and 9 spatial factors (SF) were retained. We focused on factors located in pre-frontal/frontal regions or centro-posterior regions.² Based on visual inspection of the timing and topography of the factors, six anterior and four posterior factors were of particular interest to the goals of this study. Fig. 3 depicts topographic maps of each of the pertinent PCA factors.

3.3.2.1. Anterior factors: TF4SF1 peaked at 144 ms at electrode site C22 (near Fz) and accounted for 4.58% of the total variance and 59.02% of the variance within TF4. TF6SF1 peaked at 195 ms at electrode site C22 and accounted for 2.98% of the total variance and 62.47% of the variance within TF6. TF3SF2 peaked at 308 ms at electrode site FP2 and accounted for 3.19% of the total variance and 29.54% of the variance within TF3. TF2SF1 peaked at 491 ms at electrode site C15 (between FPz and Fz) and accounted for 9.31% of the total variance and 38.47% of the variance within TF2. TF5SF2 peaked at 659 ms at electrode site FPz and accounted for 2.10% of the variance and 42.31% of the variance

²Posterior factors of interest did not include any factors peaking at, or near, the Oz electrode site because they accounted for <2% of the variance.

within TF5. TF1SF2 peaked at 808 ms at electrode site FPz and accounted for 5.04% of the variance and 18.10% of the variance within TF1.

A 6 anterior factor $\times$ 3 age group repeated measures ANOVA revealed a factor $\times$ age group interaction, $F(10,390) = 3.52, p = .001, \eta^2 = .08$. One-way ANOVAs were run for each of the factors to determine which demonstrated differences across age groups. There were amplitude differences between groups for the 195 ms, $F(2,78) = 12.48, p < .001, \eta^2 = .24$; 308 ms, $F(2,78) = 14.84, p < .001, \eta^2 = .28$; and 491 ms, $F(2,78) = 8.00, p = .001, \eta^2 = .17$, factors; and a marginal effect (after accounting for multiple comparisons) for the 659 ms factor, $F(2,78) = 4.15, p = .02, \eta^2 = .10$. For the 195 ms factor, the young and middle-aged groups generated smaller amplitudes than the old group ($ps < .002$), but did not differ from each other ($p = .24$). For the 308 ms and 491 ms factors, young adults generated smaller amplitudes than the middle-aged and old groups ($ps < .005$), who did not differ from each other ($ps > .44$). For the 659 ms factor, young adults generated smaller amplitudes than middle-aged adults ($p = .005$); old adults generated amplitudes that did not differ from either young ($p = .21$) or middle-aged adults ($p = .10$). There was no reliable difference between groups for the 144 ms factor, $F(2,78) = 2.16, p = .12, \eta^2 = .05$; however, the pattern was similar to that of several of the other anterior factors ($Y < M, p = .06, Y < O, p = .09, M = O, p = .83$) (Fig. 4).

3.3.2.2. Posterior factors: TF3SF1 peaked at 308 ms at electrode site D15 (adjacent to Cz) and accounted for 3.60% of the variance and 33.33% of the variance within TF3. TF2SF2 peaked at 491 ms at electrode site Pz and accounted for 8.21% of the total variance and 33.93% of the variance within TF2. TF5SF1 peaked at 659 ms at electrode site CPz and accounted for 3.14% of the total variance and 42.32% of the variance within TF5. TF1SF1 peaked at 808 ms at electrode site B2 (between Cz and Pz) and accounted for 11.75% of the total variance and 42.19% of the variance within TF1.

A 4 posterior factor $\times$ 3 age group repeated measures ANOVA revealed a factor $\times$ age group interaction, $F(6,234) = 4.77, p < .001, \eta^2 = .11$. One-way ANOVAs were run for each of the component factors to determine which demonstrated differences across age groups. There were amplitude differences between groups for the 659 ms, $F(2,78) = 9.24, p < .001, \eta^2 = .19$; and 808 ms, $F(2,78) = 7.52, p = .001, \eta^2 = .16$; factors, and a marginal effect for the 491 ms factor, $F(2,78) = 3.23, p = .05, \eta^2 = .08$. For the 491 ms factor, the young group generated larger amplitudes than the old group ($p = .01$), with no difference between either the young and middle-aged subjects ($p = .15$) or the middle-aged and old subjects ($p = .30$). For the 659 ms and 808 ms, young adults generated larger amplitudes than middle-aged and old subjects ($ps < .03$) who did not differ from each other ($ps > .10$)^{3,4} (Fig. 4).

³The anterior and posterior factors reported in this paper represented components with positive, not negative, amplitudes. All of the factors representing negative activity accounted for <2% of the variance.

⁴We carried out 2 factor $\times$ 3 age group repeated ANOVAs, which demonstrated a significant interaction between factor and age group for all of the analyses run: Anterior 195 ms vs. Posterior 659 ms: factor $\times$ age group: $F(2,78) = 21.11, p < .001$; Anterior 195 ms vs. Posterior 808 ms: factor $\times$ age group: $F(2,78) = 18.10, p < .001$; Anterior 308 ms vs. Posterior 659 ms: factor $\times$ age group: $F(2,78) = 25.80, p < .001$; Anterior 308 ms vs. Posterior 808 ms: factor $\times$ age group: $F(2,78) = 18.70, p < .001$; Anterior 491 ms vs. Posterior 659 ms: factor $\times$ age group: $F(2,78) = 18.48, p < .001$; Anterior 491 ms vs. Posterior 808 ms: factor $\times$ age group: $F(2,78) = 19.52, p < .001$. These results confirm that the pattern of age-related changes differed reliably between anterior and posterior factors.

3.4. Correlations

Exploratory correlation analyses were run to determine the relationship between the size of pertinent PCA factors and the following variables: age, task accuracy, mean RT, and executive capacity. See Table 3 for a summary of the significant statistical results. For anterior factors, the 195 ms, 308 ms, and 491 ms factors all correlated with age, such that the older the subject, the larger the amplitude of the factor. The 144 ms and 195 ms factors correlated with task accuracy, such that the larger the amplitude of the factor, the higher the accuracy. For the posterior factors, the 491 ms, 659 ms, and 808 ms factors each inversely correlated with age. Only the 491 ms factor correlated with RT, such that the larger the amplitude, the shorter the RT. No factors correlated with executive capacity.

We also examined the relationships between anterior and posterior PCA factors. All but one of the correlations between factors were positive, such that the larger the anterior factor, the larger the posterior factor (Supplemental Table 1). All of these correlations survived controlling for age except the one negative correlation (Supplemental Table 2).

4. Discussion

One of the major goals of this study was to identify when along the information processing stream older subjects recruit increased frontal activity. Time course analysis indicated that age-associated enhancement of anterior activity takes place between ~150 and 600 ms and age-associated decline in posterior activity is observed between ~550 and 800 ms. PCA further supported these results.

The PCA identified five separate anterior factors between 140 and 500 ms. This confirms the ability of PCA to parse variance in the waveforms that are not easily detected by simple visual inspection. When reviewing the grand average waveforms, one can readily identify two positive anterior components that have been well-characterized in the literature (the P2 and the P3a). Establishing the functional significance of the remaining components identified by the PCA would require experimental paradigms that manipulate a range of variables, allowing investigators to map the pattern of responsiveness for each component. However, consistent with prior research, several provisional inferences can be made. The results suggest that the age-related increase in anterior activity does not begin during the time in which early sensory-perceptual processing of visual stimuli is occurring in posterior brain regions.⁵ Based on previous work (Alperin et al., 2014b; Daffner et al., 2015), we suspect that the 144 ms and 195 ms factors reflect early and late anterior P2 activity and that the 491 ms factor reflects anterior P3a activity. There is evidence that the anterior P2 component indexes the motivational salience of a stimulus based on task-relevant features (Daffner et al., 2015; Luck & Hillyard, 1994; Potts & Tucker, 2001; Riis et al., 2009), and the anterior P3a component indexes the orienting or focusing of attention to execute a task (Barcelo, Escera, Corral, & Perianez, 2006; Daffner et al., 2003). This pattern of results suggests that the age-associated increase in the recruitment of anterior processing

⁵Of note, there was one early negative anterior factor that peaked at 105 ms and probably represented the anterior N1 component. Although this factor did not account for a large enough portion of the variance to be included in this paper (0.6%), there were no age-related amplitude differences for this factor. This result further supports the observation that age-related augmentation of anterior activity does not occur during the period in which early sensory processing is carried out.

mechanisms occurs after initial processing of a visual stimulus and may be specific to the operations in which attention is being marshaled to evaluate a visual event. Additional research is needed to determine whether middle-aged and older adults recruit more anterior resources than younger adults to compensate for suboptimal performance of earlier perceptual processing (Alperin et al., 2013). Moreover, studies that manipulate task difficulty can address whether this compensatory response would fail to keep performance high when subjects are faced with more challenging demands.

The age-associated augmentation of anterior neural activity appears to finish around the onset of the P3b component, which also seems to mark the start of diminished posterior activity. We found an age-related reduction in the size of the factor representing the P3b component (TF2SF2, 491 ms) and posterior slow wave components (TF5SF2, 659 ms and TF1SF1, 808 ms). Our finding of diminished late posterior activity in older adults is consistent with many reports in the literature that have highlighted reduced amplitude of late components indexing operations involved in decision making/updating or recollection (Ally et al., 2008; Anderer et al., 1996; Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006; Davis et al., 2008; Fjell & Walhovd, 2001; Wolk et al., 2009). The P3b component has been interpreted as indexing categorization/decision making, the updating of working memory once an event has been categorized, or the bridge between stimulus evaluation and response selection (Daffner et al., 2011a; Donchin & Coles, 1988; Kok, 2001; Verleger, 2008). Posterior slow wave activity may reflect continued processing of a stimulus after initial categorization (Ruchkin, Sutton, Kietzman, & Silver, 1980), the storage/rehearsal aspects of working memory (Kok & de Jong, 1980; Rushby, Barry, & Doherty, 2005), or the sustaining of attention and effort (Ruchkin et al., 1980; Rushby et al., 2005). In keeping with these kinds of interpretations, it would appear that middle-aged and old subjects recruit fewer resources for stimulus categorization, post-decision monitoring, and preparation for the next trial than their young adult counterparts.

Our finding of an age-associated decline in posterior activity and increase in anterior activity is consistent with the basic tenets of the posterior-anterior shift in aging (PASA) hypothesis (Davis et al., 2008). However, our results conflict with one aspect of this theory that suggests high-order cognitive processing linked to frontal functioning may come on-line in response to deficiencies in posterior brain areas, including ones involved in early visual operations. The sequence of information processing operations in our study indicate that reductions in posterior activity manifest after, not before, the augmentation in anterior activity. Additionally, we found positive correlations between the amplitude of several anterior and posterior factors, such that the larger the components anteriorly, the larger the components posteriorly (Supplemental Tables 1 and 2). This finding may reflect an internal consistency in the amount of resources an individual appropriates to carry out a task (Mott, Alperin, Holcomb, & Daffner, 2014). Of note, our results did not include an analysis of early sensory processing in posterior visual regions because this ERP activity explained very little of the overall variance in the principal component analysis. Unfortunately, we cannot address this issue by relying on findings in the literature about age-related differences in the size of the posterior P1 and N1 components. Results have been inconsistent, with reported increases, decreases, or no change in the amplitude of these early posterior components (Ceponiene, Westerfield, Torki, & Townsend, 2008; Curran, Hills, Patterson, & Strauss,

2001; Falkenstein, Yordanova, & Kolev, 2006). Future research is needed to deal with this important issue as well as the potential impact of age-related delays in early visual operations on later stages of information processing (Alperin et al., 2013).

Additional work is also required to determine the extent to which our pattern of findings is specific to the visual oddball paradigm used in the current study. Although the task placed demands on working memory, these demands were relatively static. Targets letters were not cued for each trial, which would have led to the ongoing need to hold updated information on-line in anticipation of upcoming stimulus presentations. Thus, the neural responses measured could be interpreted as being more reactive (to presented stimuli) than proactive. There is evidence that older adults may not proactively recruit more anterior neural activity during periods in which they are anticipating stimuli, for example, in response to unpredictable cue switches (Kopp, Lange, Howe, & Wessel, 2014) (but see De Sanctis et al., who found that high performing older subjects generate increased anterior activity in response to predictable switch cues). Our results could be interpreted as consistent with the hypothesis that older subjects are more likely to exhibit augmented anterior activity when reacting to presented stimuli than when anticipating future events. This account is supported by the fact that we did not find an increased allocation of anterior resources late in the processing stream when, as discussed above, operations are engaged that facilitate preparation for the upcoming trial.

In contrast to other studies suggesting that an increase in anterior activity in older adults may be due to frontal lobe dysfunction (Fabiani et al., 1998), and may also be specific to older adults with lower executive capacity (West et al., 2010) or task accuracy (Lorenzo-Lopez et al., 2007), we did not find any indication that larger potentials at anterior sites were associated with worse executive functioning or task performance. In fact, a few of the anterior factors correlated with increased accuracy, which argues against this age-related augmentation in neural response as representing a detrimental process. The reasons contributing to the difference between our results and others reported in the literature remain to be determined. Potential explanations for this discrepancy include the kind of task executed, type of analyses performed on the data, or specific subjects selected. Our efforts to match subjects for several pertinent variables reduced the likelihood of confounds due to the age groups differing in IQ, education, executive capacity, or task performance.

The current study expanded on previous research, which has found that older adults utilize more anterior resources than younger adults, by including subjects ranging in age from 19 to 79 and analyzing age-related differences across the processing stream. An age-associated increase in anterior function seems to be the most prominent after basic sensory processing has taken place and before final decision making and updating operations occur. The increase in anterior processing began as early as middle-age, was sustained through old age, and appeared to be linear in nature. Although middle-aged subjects most often generated responses similar to those of older adults, they occasionally exhibited patterns more like those of young adults. This finding demonstrates the importance of studying middle-age subjects to obtain a greater understanding of the transition between the presumed optimal processing of young adults and less optimal processing of older adults. The current study focused on responses to attended target stimuli. Future work should investigate the age-

related changes in response to to-be-ignored stimuli as well. Participants between 30 and 40 years old were not included in the study and may be a group in which critical age-related transitions take place. Future research should include this age group as well as adults over the age of 80 to determine the extent to which the pattern of age-related augmentation of anterior activity and reduction of posterior activity continues into old-old age.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Fig. 1.
Illustration of an experimental run.

Fig. 2. Illustration of the grand average ERP waveforms in response to target stimuli at (a) anterior and (b) posterior sites.

Fig. 3. Waveforms and scalp topographies of each of the (a) anterior and (b) posterior PCA factors in response to target stimuli. Please note that the scales used differ across factors.

Fig. 4.

Bar graphs depicting the mean $\pm$ SEM amplitude for each of the (a) anterior and (b) posterior PCA factors within in age group.

Table 1

Subject characteristics, accuracy, and mean RT (mean (SD)).

	Young	Middle-aged	Old
Number of subjects	26	26	29
Gender (male:female)	13:13	11:15	14:15
Age (years)**	22.58 (2.21)	50.92 (6.48)	72.83 (3.85)
Executive capacity (% ile)	67.38 (16.74)	69.38 (16.90)	68.61 (15.87)
Years of education	15.15 (1.54)	16.67 (5.53)	16.19 (3.20)
AMNART (estimated IQ)	116.73 (6.68)	118.54 (8.35)	118.31 (9.77)
MMSE*	29.85 (.37)	29.31 (.79)	29.41 (.82)
Accuracy (%)	88.25 (7.45)	90.69 (7.39)	91.26 (7.58)
Mean RT (ms)	610 (52)	631 (75)	644 (60)

Executive capacity = Average (composite) percentile performance (relative to published age-matched norms) 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.

Accuracy = % target hits – % false alarms.

* Effect of age group, $p < .05$ (young > middle-aged = old).

** Effect of age group, $p < .001$ (young < middle-aged < old).

Table 2

Time course analysis by 50 ms epochs for anterior (Fz cluster) and posterior (Pz cluster) sites.

		100–150	150–200	200–250	250–300	300–350	350–400	400–450
Fz cluster	<i>p</i> value	ns	.001	<.001	<.001	.001	.001	<i>a</i>
	η^2	.05	.17	.22	.18	.17	.18	.08
	Pattern	–	Y<M = O	Y = M<O	Y<M = O	Y < M = O	Y < M = O	–
Pz cluster	<i>p</i> value	ns	ns	ns	ns	ns	ns	<i>a</i>
	η^2	.04	.05	.06	.03	.05	.06	.09
	pattern	–	–	–	–	–	–	–

		450–500	500–550	550–600	600–650	650–700	700–750	750–800
Fz cluster	<i>p</i> value	<i>a</i>	.004	<i>a</i>	ns	ns	ns	ns
	η^2	.10	.13	.11	.06	.04	.03	.03
	Pattern	–	Y<M = O	–	–	–	–	–
Pz cluster	<i>p</i> value	<i>a</i>	<i>a</i>	.003	<.001	<.001	.003	.002
	η^2	.08	.08	.14	.18	.18	.14	.15
	Pattern	–	–	Y>M = O	Y > M = O	Y > M = O	Y > M = O	Y > M = O

^a Marginal effect of age group after controlling for multiple comparisons.

Table 3

Significant correlations between factors and accuracy, mean RT, executive function, and age.

	Factor	<i>r</i>	<i>p</i>	<u>Controlling for age</u>	
				<i>r</i>	<i>p</i>
Accuracy	144 ^a ms	0.28	0.01	0.27	0.02
	195 ^a ms	0.3	0.008	0.27	0.02
Mean RT	491 ^p ms	−0.26	0.02	−0.22	0.05
Age	195 ^a ms	0.46	<.001	–	–
	308 ^a ms	0.46	<.001	–	–
	491 ^a ms	0.39	<.001	–	–
	491 ^p ms	−0.27	0.02	–	–
	659 ^p ms	−0.45	<.001	–	–
	808 ^p ms	−0.41	<.001	–	–

^a Anterior.^p Posterior.