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Age-related differences in early novelty processing: Using PCA to parse the overlapping anterior P2 and N2 components

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Abstract

Previous work demonstrated age-associated increases in the anterior P2 and age-related decreases in the anterior N2 in response to novel stimuli. Principal component analysis (PCA) was used to determine if the inverse relationship between these components was due to their temporal and spatial overlap. PCA revealed an early anterior P2, sensitive to task relevance, and a late anterior P2, responsive to novelty, both exhibiting age-related amplitude increases. A PCA factor representing the anterior N2, sensitive to novelty, exhibited age-related amplitude decreases. The late P2 and N2 to novels inversely correlated. Larger late P2 amplitude to novels was associated with better behavioral performance. Age-related differences in the anterior P2 and N2 to novel stimuli likely represent age-associated changes in independent cognitive operations. Enhanced anterior P2 activity (indexing augmentation in motivational salience) may be a compensatory mechanism for diminished anterior N2 activity (indexing reduced ability of older adults to process ambiguous representations).

Keywords

Aging; Novelty; Anterior P2; Anterior N2; Motivational Salience; Mismatch; PCA

Introduction

Although the early processing of novel visual events has been the subject of ongoing study, critical questions remain about the ways in which these processes change with age. The high temporal resolution of event-related potentials (ERPs) makes this an ideal method for

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studying early processing stages. There are two major early ERP components that reflect different cognitive operations potentially important for the processing of visual novelty: the anterior P2 component, a frontally distributed positivity peaking between 150 and 250 ms, and the anterior N2 component, a frontally distributed negativity peaking between 250-350 ms.

There is evidence that the anterior P2 component serves as an index of the motivational salience of a stimulus (Potts, 2004; Riis et al., 2009) and reflects activity of the orbitofrontal cortex (OFC) (Potts & Tucker, 2001). The OFC helps to decode and anticipate the reward value of sensory stimuli and objects (Kringelbach & Rolls, 2004; Rolls, 1996), and serves as a major node in the salience network (Seeley et al., 2007). Consistent with its role in marking motivational salience, the amplitude of the anterior P2 component has been shown to be sensitive to features specified by instructions as task relevant (Luck & Hillyard, 1994; Potts & Tucker, 2001). There also are reports that stimuli that are perceptually novel (e.g., highly unusual figures and shapes) elicit a large anterior P2, especially in older adults (Beck, Swanson, & Dustman, 1980; Riis et al., 2009; Riis et al., 2008; Snyder & Hillyard, 1979). One hypothesis to account for the age-related increase in the anterior P2 to novel stimuli is that it represents the inability of older adults to inhibit the allocation of resources to non-target stimuli that should not be considered motivationally salient (Alain & Woods, 1999; Amenedo & Diaz, 1998; Gazzaley, Cooney, Rissman, & D'Esposito, 2005; Rabbitt, 1965). Against this interpretation is the finding from a study in our lab that cognitively lower performing old adults, presumably with reduced capacity to inhibit the processing of task-irrelevant non-targets, do not generate a larger anterior P2 to novel stimuli than their cognitively high performing counterparts (Riis et al., 2009). However, in this study old subjects were divided according to their composite performance on neuropsychological tests of multiple cognitive domains, leaving open the possibility of a different outcome if old adults were split in terms of performance on tests emphasizing executive function (West, Schwarb, & Johnson, 2010).

We have proposed a broader account of the functional significance of the anterior P2 component by suggesting that motivational salience can reflect top-down, controlled processes that designate certain features or combinations of features as having potential significance to an individual on the basis not only of task demands but also intrinsic reward value (Corbetta & Shulman, 2002; Daffner et al., 2003; Riis et al., 2009). Novel events have been characterized as intrinsically motivating (Berlyne, 1960; Hunt, 1965; Kakade & Dayan, 2002; Schultz, 1998), presumably related to their importance to the adaptive capacity and survival of an organism (Daffner et al., 2003; Daffner, Scinto, Weintraub, Guinessey, & Mesulam, 1994; Hunt, 1965). It remains an open question whether the enhanced early anterior positive activity sensitive to target and novel stimuli represents the same ERP component or reflects different components that overlap in time and spatial distribution. Moreover, the explanation and functional significance of the age-related increase in anterior P2 activity to novel events remains uncertain.

The mismatch anterior N2 component is also relevant to the processing of novel visual stimuli. Folstein and Van Petten (2008) make a clear distinction between the mismatch- and control- related N2 component, as summarized in their review article on the subject. The

control-related N2 is elicited by experimental paradigms that involve response conflict and inhibition, or strategic performance monitoring (Daffner et al., 2000; Folstein & Van Petten, 2008). In contrast, the mismatch-related N2 serves as an early marker of a discrepancy between the current stimulus and stored representations (Daffner et al., 2000; Ferrari, Bradley, Codispoti, & Lang, 2010; Nittono, Shibuya, & Hori, 2007; Tarbi, Sun, Holcomb, & Daffner, 2011). The mismatch N2 can be elicited by simple visual stimuli that deviate from immediate context. However, the current study focuses on the generation of this component in response to highly unusual, perceptually novel stimuli that deviate from long term experience.

Although investigations of the neural generators of the mismatch N2 have been much less common than those of the control N2, ERP source analysis and functional imaging studies have highlighted the critical role of the anterior cingulate cortex (ACC) in conflict monitoring of both motor and sensory representations. The mismatch N2 appears to reflect the activity of the ACC, a structure hypothesized to monitor for a mismatch between a presented stimulus and an established mental template, and signal a violation of expectancy (Wessel, Danielmeier, Morton, & Ullsperger, 2012). Studies also have suggested a contribution of occipital and inferior temporal regions to the generation of the mismatch-related N2, which may represent a sensory discrepancy in the visual modality or reflect the increased complexity of novel visual stimuli (Kropotov, Ponomarev, Hollup, & Mueller, 2011; Wessel et al., 2012).

Research has indicated that the anterior N2 elicited in sequential matching, standard oddball, or search tasks requires focal attention and its amplitude is strongly influenced by both the task relevance of a mismatching feature, and the frequency of a stimulus presentation (Folstein & Van Petten, 2008; Fu, Fan, & Chen, 2003; Patel & Azzam, 2005; Wang et al., 2003). In contrast, studies have demonstrated that the anterior N2 in response to perceptually novel stimuli often is not modulated by stimulus context or attention (Chong et al., 2008; Daffner et al., 2000; Schomaker, Roos, & Meeter, 2014; Tarbi et al., 2011), and can be enhanced when novel stimuli occur outside the focus of attention (Schomaker & Meeter, 2014). Moreover, in a study that varied whether frequent standard, rare target, or rare non-target stimuli consisted of simple geometric shapes or highly unusual figures, stimulus frequency and deviance from immediate context were found to have only limited influence over the size of the anterior N2. This component was most sensitive to deviation from long-term contexts that render a visual stimulus unusual and difficult to recognize (Daffner et al., 2000).

In line with work from other laboratories, we have shown that in response to novel visual stimuli both the anterior P2 and the anterior N2 components¹ exhibit marked age-related differences (Riis et al., 2009). The size of the P2 increases with age (Beck et al., 1980; Riis et al., 2009; Riis et al., 2008), whereas the size of the N2 decreases with age (Czigler & Balazs, 2005; Daffner et al., 2011; Riis et al., 2009; Riis et al., 2008). In fact, we found a strong inverse relationship between the amplitude of the P2 and the amplitude of the N2 in

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¹Please note that for brevity's sake, the terms "anterior P2 component" and "P2 component" are used interchangeably, as are the terms "anterior N2 component" and "N2 component."

response to novel stimuli: the larger the P2, the smaller the N2 response, and vice versa (Riis et al., 2009). The mechanisms underlying this pattern of results remain to be determined.

One possibility is that there are age-associated changes in the processing of both the motivational salience of novel stimuli, as indexed by the anterior P2, and the mismatch between novel stimuli and stored representations, as indexed by the anterior N2. However, an alternative explanation has not yet been excluded. The pattern observed may be due to age-linked changes in the operations indexed by only one of these components, with the changes in the other a consequence of the fact that the P2 and N2 components represent spatially and temporally overlapping waveforms that peak within 100-150 ms of each other. Given the divergent polarity of these components, age-associated changes in the amplitude of one of the components (e.g., increase in size) would lead to the appearance of age-related changes of the other component that would be in the opposite direction (e.g., decrease in size) (Riis et al., 2009).

Traditional measurement of average ERP waveforms is not well suited for parsing spatially or temporally overlapping components such as the anterior P2 and N2. The ability to distinguish one component from the other is critical for determining ways in which old adults may engage cognitive operations that are different from their younger counterparts (Alperin, Mott, Rentz, Holcomb, & Daffner, 2014). To address this issue, it is necessary to employ techniques that will aid in decomposing average waveforms. In this study, 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. This method was employed as a tool for helping to establish whether there are age-associated changes in the processing of motivational salience, the operations mediating mismatch detection, or both. In addition, PCA provided a method for examining whether the anterior P2 component sensitive to task-relevant targets can be differentiated from anterior P2 activity that is responsive to intrinsically motivating novel stimuli.

The current investigation also provided an opportunity to determine whether the major findings of our earlier study (Riis et al., 2009) could be replicated using a completely different sample of subjects and different experimental paradigm. To further test whether the age-related increase in the P2 to novels represents a failure of inhibition, neuropsychological tests emphasizing executive function rather than multiple cognitive domains were used to characterize participants and assess the impact of executive capacity on relevant ERP components. To confirm that age-associated differences in early novelty processing continue to be observed in the very old, the age range of subjects was extended to 85 years old.

Methods

Participants

Subjects were recruited through community announcements in the Boston metropolitan area. 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.

Participants were from one of four age groups, labeled young (18-32 years old), middle-aged (40-60), young-old (y-old) (65-79) and old-old (o-old) (80-85). To be included in this study, participants had to 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 y-old and o-old subjects), were unable to distinguish between the color red and blue, or had a composite score in the bottom third (0-33rd percentile) relative to age-appropriate norms on a battery of neuropsychological tests (see below). Subjects in the bottom third were excluded to reduce the likelihood of including older participants suffering from mild cognitive impairments or the early stages of a dementing illness. Subjects were paid for their time.

To appropriately interpret age-related changes in neural activity, it is important 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 (Daselaar & Cabeza, 2005; Riis et al., 2008). We made an effort to match age groups in terms of overall executive capacity and processing speed. We selected tests that had well established norms across a wide range of ages. Tests included: 1) Digit Span Backward subtest of the Wechsler Adult Intelligence Scale-IV (WAIS-IV) (Wechsler, 2008); 2) Controlled Oral Word Association Test (COWAT) (Ivnik, Malec, Smith, Tangalos, & Petersen, 1996); 3) WAIS-IV Letter-Number Sequencing; 4) WAIS-IV Digit-Symbol Coding; 5) Trail-Making Test Parts A and B (Reitan & Wolfson, 1985). For each subject, percentile performance based on age-appropriate norms was derived for each task. Executive capacity was defined as the mean (composite) performance on neuropsychological tests listed above. In keeping with suggestions in the aging literature, the groups were compared according to performance relative to age-appropriate norms (i.e., percentile scores) rather than absolute scores (Daffner et al., 2007; Daselaar & Cabeza, 2005; Riis et al., 2008).

Table 1 provides a summary of subject characteristics, including education, gender, estimated IQ, and neuropsychological test performance for each group. One hundred six subjects participated in this study. There were 26 young subjects, 26 middle-aged subjects, 29 y-old subjects, and 25 o-old subjects. An additional 3 young, 6 middle-aged, 5 y-old, and 7 o-old subjects completed the experiment, but were excluded due to excessively noisy data.

A 4 age group (young, middle-aged, y-old and o-old) ANOVA was run for each of the pertinent variables. There was no effect of age group on years of education, $F(3,98) = 1.50$, $p = .22$, AMNART estimated IQ, $F(3,98) = .26$, $p = .86$, or executive capacity (percentile

based on age-appropriate norms), $F(3,98) = 1.08$, $p = .36$. There was an effect of age group for MMSE scores, $F(3,98) = 3.32$, $p = .02$, which resulted from young subjects having a higher MMSE score than middle-aged ($p = .008$) and old ($p = .009$) subjects.

Experimental Procedure

The experiment consisted of a color-selective attention, novelty oddball task in which subjects were shown a series of stimuli presented in either the color red or the color blue, and were asked to respond by button press to specific target letters. Subjects were instructed to pay attention to stimuli appearing in the designated color while ignoring stimuli 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. An ignore condition was included in this study to be able to examine the impact of attentional relevance on the anterior P2 and anterior N2, and determine if such attentional effects were modulated by age. Practice trials preceded each set of experimental trials. The attended color and the hand used for the target response were counterbalanced across subjects.

To help minimize group differences in performance, task demands were made slightly easier for old subjects. This was done to allow us to draw inferences about age-related differences in neural activity and not performance-related differences (Haring et al., 2013). 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 young and old subjects responded to 4 target letters. 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 designated upper case letters. Standard stimuli (70% overall; 35% in each color) were any non-target upper case letters. Novel stimuli (7.5% in each color) were unusual/unfamiliar line drawings, such as impossible or fragmented objects (Kosslyn et al., 1994; Kroll & Potter, 1984) shown only one time each. 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). Figure 1 depicts an experimental run. For analytic purposes, trials were further categorized in terms of whether the stimuli presented were in the attend or the ignore color.

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 the 10-20 system position Cz (see Daffner et al., 2012). 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

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). Demographic variables, percentile performance on the neuropsychological tests, and performance on the experimental task for the four groups were compared using one-way analysis of variance (ANOVA).

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 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. EEG epochs for the three stimulus types (standard stimuli, target stimuli, novel stimuli) and 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.

Analysis of Average ERP Waveforms

The latency of the anterior P2 was measured as the local positive peak latency between 100-250 ms at electrode Fz and the latency of the anterior N2 was measured as the local negative peak latency between 200-350 ms at electrode Fz. The amplitude of the P2 and the N2 was derived from the average value of the 80 ms interval centered at the mean peak latency of these two components as measured for each age group in response to each stimulus type². Based on visual inspection of the grand average waveforms and surface potential maps, amplitude was measured as the average of Fz and the nine electrode sites that clustered around it. Average ERP results were analyzed using ANOVA with stimulus type and condition as within-subject variables, and age group as the between-subject variable.

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²We elected to utilize mean, and not peak, amplitude for several reasons. The major purpose of analyzing averaged waveforms was to replicate our previously reported findings, and thus we chose to follow our prior measurement approach, which relied on mean amplitude. As Steven Luck (2005) has argued, mean amplitude measurements have several advantages over peak amplitude measurements, including being less sensitive to high-frequency noise and not being biased by the number of experimental trials. We acknowledge that there is no universally accepted method for measuring amplitude. Thus, we re-ran the analyses using local peak amplitude measurements for the P2 (100-250 ms) and N2 (200-350 ms) components. We found that the pattern of response using peak amplitude was the same as using mean amplitude, with one minor exception. Unlike the mean amplitude analysis for the N2 component, the peak amplitude analysis did not reveal an interaction between condition and age group for the N2 component.

Temporospatial Principal Component Analysis (PCA)

Temporospatial PCA is able to decompose the data to distinguish the underlying components that contribute to the grand average ERP. The temporal PCA takes advantage of the high temporal resolution of EEG. Because it can produce cleaner separation of the data than the spatial PCA, Dien (2010b) recommends running a temporal PCA first. After parsing the temporal variance into non-overlapping temporal components, the next step is to compute a spatial PCA for each identified temporal principal component, breaking them down into a series of spatially distinct components.

Following the recommendation of Dien (2012), a temporospatial PCA was conducted on each subjects' individual ERP averages at all 134 electrode sites. ERPs to novel, target, and standard stimuli under the attend and ignore conditions were included in the analysis. Utilizing the ERP PCA toolkit 2.39 (Dien, 2010a), 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. Following the literature, factors of interest were selected based on visual inspection of the timing and topography of the output (Dien, Spencer, & Donchin, 2003; Spencer, Dien, & Donchin, 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 with stimulus type and condition as within-subject variables, and age group as the between-subject variable. 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 (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. Correlation analyses were run to address specific questions of interest to the goals of the study, such as whether in response to novel stimuli there was an inverse relationship between the size of the anterior P2 and the size of the anterior N2. If significant, the analyses were re-run after controlling for age.

Results

Behavior

Target accuracy and mean reaction time (RT) data are presented in Table 2. For accuracy, a 4 age group ANOVA revealed no effect of age group, $F(3,101) = .87$, $p = .46$. In terms of RT, there was a marginal effect of age group, $F(3,101) = 2.58$, $p = .06$, which resulted from young subjects having shorter RTs than old subjects ($p = .009$).

ERPs

Traditional Analyses—Figure 2 illustrates the grand average waveforms for the cluster of anterior electrode sites (Fz and the surrounding 9 sites³) in response to each stimulus type under the attend condition for each age group. The surface potential maps in response to

³All of the analyses reported were re-run at Fz alone, which yielded an identical pattern of results.

novel stimuli for the anterior P2 and the anterior N2 are presented in Figure 3. Supplementary Figure 1 depicts the surface potential maps in response to standard and target stimuli. Supplementary Tables 1 and 2 provide the means and SDs for the amplitude and latency of the P2 and N2 components, respectively, for each stimulus type across the four age groups and two conditions.

Anterior P2—For the mean amplitude of the anterior P2 component, there were effects of stimulus type, $F(2,204) = 15.12$, $p < .001$, condition, $F(1,102) = 28.37$, $p < .001$, and age group, $F(3,102) = 8.77$, $p < .001$, and an interaction between age group and stimulus type, $F(6,204) = 3.44$, $p = .007$. The effect of stimulus type was due to the amplitude of the P2 being larger to target stimuli than to standard ($p < .001$) or novel stimuli ($p < .001$), with no difference between the latter two. The effect of condition was due to the amplitude of the P2 being larger under the attend than the ignore condition. The effect of age group was due to young adults having a smaller P2 amplitude than the other age groups (all p 's $< .003$), who did not reliably differ from one another. The age group $\times$ stimulus type interaction was due to the magnitude of the age group effect being largest in response to novel stimuli (η^2 : novels = .24; standards = .17; targets = .16). (Supplementary Figure 2a is a bar graph depicting mean amplitude of the P2 for each stimulus type across the four subjects groups and two conditions.)

For the anterior P2 latency, there was an effect of stimulus type, $F(2,204) = 5.64$, $p = .005$, and a trend toward an effect of age group, $F(3,102) = 2.67$, $p = .05$. The stimulus type effect was due to the P2 in response to novel stimuli peaking later than to standards ($p < .01$) and targets ($p < .01$), with no difference between the latter two. The trend toward an age group effect was due to the P2 of middle-aged subjects peaking earlier than the P2 of y-old ($p < .02$) and o-old subjects ($p < .03$). There was a stimulus type $\times$ age group interaction, $F(6,204) = 3.97$, $p = .001$. This finding was due to no age-related differences in P2 latency in response to standard or target stimuli, but an effect of age group in response to novel stimuli, $F(3,102) = 9.64$, $p < .001$, which was present because young and middle-aged subjects exhibited a shorter P2 latency to novels than y-old and o-old subjects (all p 's $< .002$).

Anterior N2—In terms of the anterior N2 amplitude, there were effects of stimulus type, $F(2,204) = 288.93$, $p < .001$, condition $F(1,102) = 7.55$, $p = .007$, and age group, $F(3,102) = 10.51$, $p < .001$, and interactions between stimulus type and age group, $F(6,204) = 4.43$, $p = .002$, and condition and age group, $F(3,102) = 4.42$, $p = .006$. The effect of stimulus type was present because the size of the N2 was larger (i.e., more negative) in response to novel than standard stimuli ($p < .001$), which in turn was larger than in response to target stimuli ($p < .001$). The effect of age group resulted from young adults having a larger N2 amplitude than the other age groups (p 's $< .001$), all of whom did not differ reliably from one another. The stimulus type $\times$ age group interaction was due to the magnitude of the age group effect being largest in response to novel stimuli (η^2 : novels = .29; standards = .14; targets = .15). The effect of condition was due to the amplitude of the N2 being smaller under the attend than the ignore condition, an effect that was modified by age. For y-old subjects, N2 was smaller under attend than ignore ($p = .007$), whereas there were no reliable differences between conditions for the other age groups. (See Supplementary Figure 2b, a bar graph depicting the

mean amplitude of the N2 for each stimulus type across the four subjects groups and two conditions.)

For anterior N2 latency, there was an effect of stimulus type, $F(2,204) = 6.88$, $p = .001$, and age group, $F(3,102) = 7.02$, $p < .001$, and a stimulus type $\times$ age group interaction, $F(6,204) = 7.24$, $p < .001$. The stimulus type effect was due to the N2 latency for target stimuli being earlier than the latency for novel ($p < .009$) or standard stimuli ($p < .001$). The age group effect was due to young subjects having an earlier N2 latency than y-old subjects ($p = .02$), and middle-aged subjects having an earlier N2 latency than y-old ($p < .001$), and o-old ($p < .003$) subjects. The stimulus type $\times$ age group interaction resulted from there being an age group effect for both standard stimuli ($p < .001$), with middle-aged subjects exhibiting an earlier N2 latency than y-old ($p < .001$) and o-old ($p < .003$) subjects, and novel stimuli ($p < .001$), with young and middle-aged subjects exhibiting an earlier N2 latency than y-old and o-old subjects (p 's $< .001$).

Correlations—In keeping with the goals of this study, we examined the relationship between the amplitude of the anterior P2 and anterior N2 in response to novel stimuli, and found a strong correlation, $r(104) = .47$, $p < .001$, that survived after controlling for age $r(103) = .33$, $p = .001$. As the amplitude of the P2 increased, the amplitude of the N2 decreased.

Principal Component Analysis (PCA)—A temporospatial PCA yielded 135 factor combinations (15 temporal factors, each with 9 spatial factors). One hundred five of the factor combinations were not analyzed further because each accounted for $< 0.5\%$ of the total variance and were assumed to reflect noise. The initial temporal PCA yielded 14 temporal factors (TF) that accounted for 94.95% of the variance. We focused on factors during the temporal interval of the P2 (100-250 ms) and N2 (200-350 ms). There were two temporal factors which occurred within the appropriate temporal window of the P2, one peaking at 152 ms (TF4), which accounted for 7.42% of the variance, and one peaking at 202 ms (TF7), which accounted for 4.94% of the variance. There was one temporal factor that occurred within the temporal window of the anterior N2, peaking at 304 ms (TF3), which accounted for 16.47% of the variance.

A spatial PCA was performed on TF4 and nine spatial factors (SF) were retained. Based on visual inspection of the timing and topography of the factors, one (TF4SF1) was of particular interest to the goals of this study, as it reflected a positivity with an anterior distribution, consistent with the topography of the anterior P2. TF4SF1 accounted for 4.40% of the total variance and 59.30% of the variance within TF4. We will label TF4SF1 as the “early anterior P2.” A spatial PCA was performed on TF7 and nine spatial factors (SF) were retained. One factor, TF7SF1, reflected a positivity with an anterior distribution, consistent with the topography of the anterior P2. TF7SF1 accounted for 3.19% of the total variance and 64.57% of the variance within TF7. We will label TF7SF1 as the “late anterior P2.” Finally, a spatial PCA was performed on TF3 and nine spatial factors were retained. One was of particular interest given its negativity and anterior distribution, consistent with the topography of an N2. The TF3SF1 accounted for 8.56% of the total variance and 51.97% of the variance within TF3. We will label TF3SF2 as the anterior N2. Of note, temporospatial

PCA was repeated first on the data for each age group separately and then on the data for each stimulus type separately. These analyses revealed that each age group had the same component structure, and each stimulus type elicited the same component structure, which included an early anterior P2 factor, a late anterior P2 factor, and an anterior N2 factor. These data are not reported here.

Early Anterior P2 (TF4SF1)

Figure 4a depicts the topography and amplitude of TF4SF1 for each age group in response to standard, target, and novel stimuli under the attend condition. Supplementary Figure 3a is a bar graph showing the factor scores (amplitudes) of the TF4SF1 for each stimulus type, across the 4 subject groups and 2 conditions, and Supplementary Table 3 presents the means and SDs for this dataset. A 3 stimulus type (standards, targets, novels) x 2 condition (attend, ignore) x 4 age group (young, middle-aged, y-old, o-old) ANOVA revealed effects of stimulus type, $F(2,204) = 56.44$, $p < .001$, condition, $F(1,102) = 14.03$, $p < .001$, and age group, $F(3,102) = 3.23$, $p = .03$. The effect of stimulus type was due to targets eliciting a larger early P2 than standards ($p < .001$), which, in turn, elicited a larger response than novels ($p < .001$). The condition effect was due to the size of the early P2 response being larger under the attend than the ignore condition. This effect was not modulated by age group. The age group effect resulted from the early P2 generated by the young adults being smaller than that generated by other age groups (all p 's $< .016$), who did not reliably differ from one another.

Late Anterior P2 (TF7SF1)

Figure 4b depicts the topography and amplitude of TF7SF1 for each age group in response to standard, target, and novel stimuli under the attend condition. Supplementary Figure 3b is a bar graph illustrating the amplitude of the TF7SF1 for each stimulus type, across the 4 subject groups and 2 conditions, which is also presented in a tabular format in Supplementary Table 3. A 3 stimulus type x 2 condition x 4 age group ANOVA demonstrated effects of condition, $F(1,102) = 30.47$, $p < .001$, and age group, $F(3,102) = 17.99$, $p < .001$, and an interaction between stimulus type and age group, $F(6,204) = 13.81$, $p < .001$. The effect of condition was present because the size of the late P2 factor was larger under the attend than the ignore condition, which was not modified by age group. The age group effect was due to an age-related increase in the size of the late P2 [young $<$ middle-aged ($p = .013$) $<$ y-old ($p < .001$) $=$ o-old ($p = .514$)]. The stimulus type x age group interaction can be explained by the magnitude of the age-related differences being largest in response to novel stimuli (η^2 : novels = .43; standards = .23; targets = .23). The interaction between stimulus type and age group can also be explained by a different pattern of response to the various stimulus types across age groups. For young adults, the effect of stimulus type, $F(2,50) = 12.08$, $p < .001$, was present because the late P2 was smaller in response to novels than standards ($p = .001$) or targets ($p = .003$), with no difference between the latter two stimulus types. For middle-aged adults, the size of the late P2 did not differ across stimulus types, $F(2,50) = .83$, $p = .41$. In contrast, the effect of stimulus type for yold, $F(2,56) = 10.35$, $p = .001$, and o-old adults, $F(2,48) = 18.06$, $p < .001$, was due to the size of the late P2 being larger for novels than targets or standards (all p 's $< .005$), with no difference between the latter two stimulus types.

Early vs. Late Anterior P2

To examine whether the pattern of response differed reliably between the early and late anterior P2, a 2 component type (early anterior P2, late anterior P2) x 3 stimulus type x 2 condition x 4 age group ANOVA was run. Our focus was on whether there was an interaction between component type and the other variables. There were interactions between component type and age group, $F(3,102) = 4.38$, $p = .006$, component type and stimulus type, $F(2,204) = 41.68$, $p < .001$, and component type, stimulus type, and age group, $F(6,204) = 17.02$, $p < .001$. The interaction between component type and age group was present because the magnitude of the age effect was larger for the late P2 than the early P2 (η^2 : late P2 = .35; early P2 = .09). This interaction can also be explained by the fact that the early P2 component was larger than the late P2 component for young, $F(1,25) = 11.47$, $p = .002$ and middle-aged, $F(1,25) = 26.63$, $p < .001$ subjects, whereas the amplitude of the two components did not differ for y-old ($p = .69$) and oold ($p = .12$) subjects. The interaction between component type and stimulus type was due to there being a stimulus type effect for the early P2 (target > standard > novel), but not for the late P2 component. The interaction between component type, stimulus type, and age group was observed because for the early P2 there was no interaction between stimulus type and age group, whereas for the late P2 there was a robust interaction between stimulus type and age group, $F(6,204) = 13.81$, $p < .001$, the pattern of which was reviewed in the section above.

Anterior N2 (TF3SF1)

Figure 4c depicts the topography and amplitude of TF3SF1 for each age group in response to standard, target, and novel stimuli under the attend condition. (See Supplementary Figure 3c, a bar graph illustrating the amplitude of the TF3SF1 for each stimulus type, across the 4 subject groups and 2 conditions, and Supplementary Table 3 for a summary of the means and SDs of this dataset.) A 3 stimulus type x 2 condition x 4 age group ANOVA revealed effects of stimulus type, $F(2,204) = 157.36$, $p < .001$, and age group, $F(3,102) = 10.02$, $p < .001$. In addition, there was an interaction between stimulus type and age group, $F(6,204) = 4.79$, $p = .001$. The effect of stimulus type was present because the amplitude of the N2 was larger (more negative) for novels than standards ($p < .001$), which, in turn, was larger than for targets ($p < .001$). The age group effect was observed because young adults generated a larger N2 than all of the other groups (all p 's < .001), who did not reliably differ from one another. The interaction between stimulus type and age group was observed because the magnitude of the age-related differences in the N2 was largest in response to novel stimuli (η^2 : novels = .26; standards = .16; targets = .16).

Correlation analyses

Correlation analyses were run to address several questions pertinent to the goals of this study. Our main focus was on responses to novel stimuli under the attend condition. The first issue examined was the relationship between age and the size of each PCA components in response to novel stimuli. Age correlated with the amplitude of the late P2 component, $r(104) = .64$, $p < .001$: the older the subject the larger (more positive) the late P2. Age also correlated with the amplitude of the N2 component, $r(104) = .33$, $p = .001$: the older the

subject, the smaller (less negative) the N2. There was no correlation between age and the amplitude of the early P2 component, $r(104) = .13$, $p = .20$.

Next, we analyzed the relationship between the size of the late P2 and the size of the N2 component. Across the entire group of subjects, the amplitude of the late P2 inversely correlated with the amplitude of the N2, $r(104) = .45$, $p < .001$, which remained significant after controlling for age, $r(104) = .31$, $p = .001$: the larger the late P2, the smaller the N2 in response to novel stimuli.

We then considered the hypothesis that the increased amplitude of the late P2 to novel stimuli among older adults represents a failure to inhibit the processing of salient task-irrelevant stimuli. If this hypothesis were true, one would expect that older subjects who perform worse on the task or have lower executive capacity would generate the largest late P2 responses to novel stimuli. Among y-old and o-old subjects, the size of the late P2 component inversely correlated with mean RT, $r(52) = -.46$, $p < .001$, and directly correlated with accuracy, $r(52) = .36$, $p = .008$, and marginally correlated with executive capacity, $r(52) = .24$, $p = .08$. These results run counter to the failure of inhibition hypothesis and suggest that, among older adults, the larger the late P2 in response to novel stimuli, the shorter the RT, the better the accuracy, and the higher the executive capacity (although the latter was only a trend).

We also determined whether, similar to the late P2, across older subjects, a larger N2 in response to novel stimuli was associated with better performance on the experimental task or tests of executive functioning. The size of the N2 component did not correlate with mean RT, $r(52) = .08$, $p = .56$, accuracy, $r(52) = -.09$, $p = .50$, or executive capacity, $r(52) = -.17$, $p = .21$. In summary, these analyses suggest that there is no correlation between the size of the N2 response to novel stimuli and RT, accuracy, or executive capacity.

Finally, the observation that older adults generated a larger early P2 to standard stimuli than their younger counterparts could be interpreted as an age-related failure to inhibit the processing of task-irrelevant stimuli. To test this hypothesis, we examined if there were relationships between the early P2 to standards and pertinent behavioral variables. Across y-old and o-old subjects, the size of the early P2 to standards inversely correlated with mean RT, $r(52) = -.45$, and directly correlated with accuracy, $r(52) = .29$, $p = .04$, and executive capacity, $r(52) = .29$, $p = .05$. Thus, among older adults, the larger the early P2 to standards, the better the task performance and the higher the executive capacity.

Discussion

The main goal of this study was to examine age-related differences in the early processing of novel visual stimuli using PCA to parse the anterior P2 and anterior N2 components both temporally and spatially. Consistent with other reports in the literature (Beck et al., 1980; Czigler & Balazs, 2005; Daffner et al., 2011; Riis et al., 2009; Riis et al., 2008), analyses of the average waveforms revealed an age-related increase in the size of the anterior P2 and an age-related decline in the size of the anterior N2. The magnitude of the age-related differences was largest in response to novel stimuli. Across subjects, the amplitude of the P2

to novel stimuli inversely correlated with the amplitude of the N2 to novel stimuli, which replicated the results of a previous study (Riis et al., 2009) using a different subject sample and experimental paradigm.

Anterior P2 components

PCA suggested that the anterior P2 observed in the average ERP waveforms reflected two temporospatial factors separated by ~50 ms: an early factor peaking ~152 ms and a late factor peaking ~202 ms. Across all age groups, the early P2 was particularly sensitive to task relevance, whereas for y-old and o-old adults, the late P2 was especially responsive to novelty. An ANOVA comparing the two temporospatial P2 factors, labeled the early and late anterior P2, underscores their inherent similarities and differences. Both the early and late P2 components exhibited an age-related increase in amplitude. However, the magnitude of this effect was much larger for the late P2. Also, the amplitude of both the early and late P2 components was substantially larger under the attend than the ignore condition, consistent with the notion that both components reflect the activity of top-down processing. This attentional effect was of similar magnitude across all age groups, which points to the relative preservation of the capacity of older adults to enhance the processing of stimuli that have task-germane features (Haring et al., 2013; Kok, 2000; Riis et al., 2009).

The 3-way interaction between component type, age, and stimulus type highlights important differences between the two P2 components. For the early P2 component, there were no age related differences in the pattern of response to the different stimulus types, with all age groups generating an early P2 that was largest in response to target stimuli. In contrast, for the late P2, the pattern of response to the three stimulus types varied across age groups. For the young adult group, the late P2 was larger for target than novel stimuli, whereas for y-old and oold subjects, the late P2 was larger for novel than target stimuli. The middle-age group appeared to exhibit a transitional pattern, with no reliable differences in the late P2 amplitude across stimulus types.

The results of the PCA help to explain conflicting reports in the literature about the functional significance of the anterior P2, which have been based upon the analysis of average waveforms. Studies limited to young adults, which have not included perceptually novel stimuli, have emphasized that the P2 is sensitive to task-relevant features and largest in response to target stimuli (Luck & Hillyard, 1994; Potts, Liotti, Tucker, & Posner, 1996; Potts & Tucker, 2001). Investigations that have incorporated older adults and included perceptually novel visual stimuli have reported an enhanced P2 response to novel events, especially among old participants (Beck et al., 1980; Riis et al., 2008; Snyder & Hillyard, 1979). The current study's PCA suggests that the varying results for the P2 component may be due to indexing the activity of two different latent factors within the P2 temporal window. We would argue that both factors reflect the motivational salience of stimuli. However, they are responsive to different aspects of motivational salience, with the early P2 sensitive to task relevance and the late P2 sensitive to the intrinsic relevance assigned to novel events.

Anterior N2 component

The anterior N2 component most relevant to the current study indexes the mismatch between the current stimulus presentation and stored representations (Folstein & Van Petten, 2008).⁴ Studies using average wave forms have demonstrated that the N2 is very sensitive to highly unusual, perceptually novel stimuli, and its response to such stimuli is relatively insensitive to direction of attention, task relevance, or frequency of stimulus presentation (Chong et al., 2008; Daffner et al., 2000; Tarbi et al., 2011). Consistent with these observations, the PCA component representing the N2 was much larger in response to novel visual stimuli than to other stimulus types, a finding evident across all age groups, and its amplitude was not influenced by attentional condition.

Age-related differences

The study demonstrated age-related increases in the size of the early and late P2 components. In contrast, it revealed age-related decreases in the size of the N2 component. Correlation analyses suggest that in response to novel stimuli there is a direct relationship between age and the size of the late P2 and an inverse relationship between age and the N2. These findings are in keeping with other reports in the literature (Beck et al., 1980; Czigler & Balazs, 2005; Riis et al., 2009; Riis et al., 2008). Moreover, there was an inverse relationship between the size of the late P2 component and the size of the N2 component in response to novel stimuli, which remained significant after controlling for age.

The current investigation helps to exclude the possibility that the age-associated differences in both the P2 and N2, which have been observed using traditional analyses of average waveforms (Riis et al., 2009), are simply driven by the spatially and temporally overlapping nature of the anterior P2 and N2 components. Temporospacial PCA allowed us to parse overlapping waveforms into their underlying components. A reasonable interpretation is that operations indexed by both the P2 and the N2 in response to novel stimuli undergo changes with aging. Specifically, there is an age-associated increase in processing the motivational salience of novelty, as well as an age-related decrease in processing the mismatch between novel stimuli and representations stored in short or long term memory. What mechanisms might account for these findings?

Age-related decrease in the anterior N2 to novel stimuli

The anterior N2 component exhibited an age-associated decline in amplitude, especially in response to novel stimuli. One potential explanation for this finding is that as individuals grow older, they interact with an increasing number of visual stimuli and develop a wider range of stored representations (Riis et al., 2009). For older adults, even visual stimuli that are seemingly unusual might be matched to an image within their large reservoir of stored representations. There is evidence that greater familiarity with the stimulus, which has been

⁴It is worth noting that it is unlikely that the enhanced N2 to novel stimuli represents a no-go (control) N2, which serves to index the increased need for motor control to prevent a response to non-target events. Although both frequent standard stimuli and infrequent novel stimuli demand no response, the novels elicited a much larger N2. One would anticipate the opposite pattern if this component represented a nogo N2 (Folstein & Van Petten, 2008). The non-target standard stimuli are letters that are much more perceptually similar to target stimuli that are letters, and should therefore generate more conflict in terms of whether to respond than the novel stimuli that are highly unusual figures and easily distinguished from target stimuli (Azizian, Freitas, Parvaz, & Squires, 2006).

labeled perceptual fluency, results in a smaller N2 component (Daffner et al., 2000; Ferrari et al., 2010). A direct experimental test of this hypothesis, as it applies to aging, is not feasible. Nevertheless, if the postulated underlying mechanism were true, one might anticipate that individuals with greater interest in, or exposure to, varying kinds of visual stimuli would generate a smaller N2 to novel stimuli. However, this finding has not been confirmed. For example, although we have demonstrated that across the adult lifespan, higher cognitive capacity is strongly associated with greater attraction to novel visual stimuli, the size of the N2 in response to novels is not modulated by cognitive status (Riis et al., 2008). Similarly, in the current study, there was no correlation between the size of the N2 to novels and executive capacity.

An alternative hypothesis is that normal aging is associated with a diminished ability to process ambiguous representations or encode unusual stimuli (Denburg et al., 2007; Falkenstein, Hoormann, & Hohnsbein, 2001; Mager et al., 2007; Zamarian, Sinz, Bonatti, Gamboz, & Delazer, 2008) like the novel stimuli presented, which included impossible, incongruous, and fragmented objects. Theoretically, this reduced ability could lead to two different outcomes. On the one hand, because the size of the N2 in response to a stimulus is inversely proportional to the ease of encoding it (i.e., perceptual fluency) (Ferrari et al., 2010), one might expect to find an age-related augmentation of this component, which was not observed. On the other hand, if aging were associated with a failure to adequately engage the operations by which visual uncertainty and conflict are processed, it could lead to a decline in the N2. This idea would be in keeping with data suggesting that older adults are less able to manage various types of conflicting representations, for example, stimuli that have incongruous or ambiguous meaning (Mayr, 2001; Monti, Weintraub, & Egner, 2010), motor programs that code for competing responses (Hammerer, Li, Muller, & Lindenberger, 2010), or mismatches between representations of erroneous and correct responses (Falkenstein et al., 2001). The relationship between age-associated changes in processing stimulus ambiguity as compared to response ambiguity remains to be determined. Of note, both kinds of processing may rely on components of a shared neural network. There is growing evidence that the control N2, which indexes conflict between competing motor signals and whose amplitude also declines in older adults (Lucci, Berchicci, Spinelli, Taddei, & Di Russo, 2013; Willemsen, Falkenstein, Schwarz, Muller, & Beste, 2011), reflects the activity of the anterior cingulate cortex (Kropotov et al., 2011; Wessel et al., 2012). This structure also appears to mediate the mismatch N2 (Kropotov et al., 2011; Wessel et al., 2012), which indexes conflict between a presented stimulus and stored representations (Falkenstein, 2006; Folstein & Van Petten, 2008).

Age-related increase in the anterior P2

One explanation for the age-associated increase in the P2 amplitude to novel stimuli is that it reflects the inability of older adults to inhibit the processing of task-irrelevant stimuli that should not be considered motivationally salient (Chao & Knight, 1997; Gazzaley et al., 2005; Rabbitt, 1965). This hypothesis would be supported by finding that older individuals with lower attentional control abilities (and thus inhibitory capacity) generate a larger P2 to novel stimuli. A previous investigation (Riis et al., 2009) that classified subjects based on an overall index of cognition did not confirm this idea. Moreover, in the current study,

correlation analyses indicated that older subjects who generated larger late P2 responses to novel stimuli actually performed better on the experimental task and tended to have higher scores on neuropsychological tests emphasizing executive function.⁵

The inverse relationship between age-related changes in the anterior P2 and anterior N2

We found a strong inverse correlation between the amplitude of the late P2 and the amplitude of the N2 in response to novel visual stimuli. It is possible that there is no direct link between the operations indexed by these two components, but that the relationship is driven by independent age-related changes associated with each component. Contrary to this account is the finding that the inverse correlation between the P2 and N2 survived controlling for age, which supports the possibility of a more causal relationship.

One explanation for the inverse correlation between the size of the P2 and N2 is that age-related augmentation in response to motivationally salient novel stimuli (as indexed by an enhanced P2) facilitates the ease of processing these novel events (as indexed by a diminished N2). However, it is unclear why aging would lead to such a processing advantage. An alternative hypothesis is that age-related increases in the top-down processing of motivational salience, as indexed by the P2, may reflect a compensatory mechanism to counter the age-associated decrease in the relatively automatic processing of a mismatch between novel stimuli and stored representations, as indexed by the N2. One concern with this hypothesis that favors compensation is that the operations indexed by the late P2 likely start before those indexed by the N2. As such, the compensatory mechanism would not represent an “on-line” reaction to impaired N2 activity in response to a particular stimulus. Rather, the augmented late P2 would reflect an overall age-related shift in strategy or approach to the processing of novel visual stimuli that compensates for compromised operations elsewhere in the processing stream. Consistent with other reports linking age-related compensatory activity to frontal-executive control mechanisms (Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Cappell, 2008), it is noteworthy that in the current study, the late P2 is modulated by top-down attentional control operations, whereas the N2 to novel events elicited in this experiment was not influenced by attentional condition. Interpreting the increase in P2 amplitude as a compensatory mechanism is strengthened by results suggesting that among older adults, larger responses are associated with superior performance and executive capacity.

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⁵We also need to address the finding of an age-related increase in the size of the early P2 to standard stimuli. This result would suggest that relative to their younger counterparts, older subjects process standards as motivationally salient, which may appear to be a failure of inhibition. There are several reasons why we have not adopted this perspective. First, among older adults, the early P2 to targets was substantially larger than to standards, with the magnitude of this stimulus effect not differing across age groups. Moreover, among older subjects, a larger early P2 to standards was associated with better task performance and higher executive functioning. These results accord with other findings from our lab, which have demonstrated an age-related augmentation of the anterior P3 component not only to rare targets, but also repetitive standards (Alperin et al., 2014; Daffner et al., 2005; Daffner et al., 2006; Riis et al., 2008). Older adults seem to approach the current task and others by treating all stimulus types as (relatively) attention-worthy (as indexed by the anterior P3a) and motivationally salient (as indexed by the P2). Although not an ideal use of limited processing resources, this approach to stimuli may serve to scaffold evaluative processing that occurs in posterior brain regions (Alperin et al., 2014), and is associated with higher cognitive functioning (as measured by neuropsychological tests) and better task performance (Riis et al., 2008).

Limitations and strengths of the study

A single PCA was applied to all four age groups and all three stimulus types. One issue is that if there were sufficient variation in the latency of components across the groups or stimulus types, the PCA could misallocate variance and identify what appear to be different components (e.g., an early and a late P2), but in fact were really the same one that peaked at different times. This matter was addressed by finding the same component structure (early P2, late P2, N2) when repeating the temporospatial PCA on the data for each age group individually and on each stimulus type separately.

Our study has many strengths, including the relatively large sample size ($n = 106$) and range of ages of our subjects (19–85 years old). The groups were well matched in terms of education, gender, estimated IQ, and executive capacity relative to age-appropriate norms, increasing the likelihood that the differences between groups in the P2 and N2 were a reflection of age and not other confounding variables.

In summary, the use of temporospatial PCA provides strong evidence for age-related differences in the processes indexed by both the anterior P2 and the anterior N2. Our results also suggest that there may be a causal link between the changes observed for these components. We propose that the age-associated augmentation of top-down operations involved in processing the motivational salience of stimuli, as indexed by the anterior P2, reflect a compensatory mechanism to counter the age-related decline in operations involved with automatically processing the mismatch or conflict between the current stimulus being presented and stored representations, as reflected in the anterior N2. Further research is needed to validate this hypothesis and examine the impact of age-related changes in the P2 and N2 on later processing stages.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

PCA was used to examine age-related changes in early ERP processing of novelty

Is the inverse relationship between anterior P2 and N2 due to temporospatial overlap?

Early and late P2, sensitive to relevance and novelty respectively, increase with age

N2 responsive to novelty decreases with age and inversely correlates with the late P2

Age-related differences in the P2 and N2 reflect changes in independent operations

Figure 1.
Illustration of an experimental run.

Figure 2.

Depiction of the grand average ERP waveforms for all 4 age groups representing the average response at Fz and the 9 electrode sites clustered around it in response to a) standard b) target, and c) novel stimuli under the attend condition. The gray bar illustrates the approximate temporal interval of the anterior P2 and the purple bar illustrates the approximate temporal interval of the anterior N2.

Figure 3.

Surface potential maps of the anterior P2 and anterior N2 components in response to novel stimuli under the attend condition. Values reflect the mean amplitude of the 80 ms interval centered at the mean peak latency, as measured for each age group in response to each stimulus type. Note that the scales differ across components.

Figure 4.

Scalp topographies and waveforms of PCA factors for all 4 age groups: a) Early Anterior P2 (TF4SF1), b) Late Anterior P2 (TF7SF1), and c) Anterior N2 (TF3SF1) in response to standard, target, and novel stimuli under the attend condition. Note that the scales differ across factors.

Table 1

Subject Characteristics (Mean(SD))

	Young	Middle	Y-Old	O-Old
Number of subjects	26	26	29	25
Age	22.58 (2.21)	50.92 (6.48)	72.83 (3.85)	82.56 (2.02)
Gender (male:female)	13:13	10:16	14:15	10:15
Years of Education	15.15 (1.54)	16.67 (2.53)	16.19 (3.20)	16.32 (3.34)
AMNART	116.73 (6.68)	118.54 (8.35)	118.31 (9.77)	119.80 (9.66)
MMSE	29.85 (.37)	29.31 (.79)	29.41 (.82)	29.32 (.95)
EC Percentile	67.38 (16.74)	69.38 (16.90)	68.61 (15.87)	76.29 (14.21)

AMNART = American National Adult Reading Test (estimated IQ)

MMSE = Mini Mental State Exam

EC = Executive capacity composite percentile score based on age-matched norms

Table 2

Accuracy and Mean RT (Mean (SD))

	Young	Middle	Y-Old	O-Old
Accuracy (%)	88.25 (7.45)	90.69 (7.39)	91.26 (7.58)	88.38 (11.46)
Mean RT (ms)	611 (52)	631 (75)	644 (60)	659 (66)