Mechanisms Underlying Age- and Performance-related Differences in Working Memory

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Abstract

■ This study took advantage of the subsecond temporal resolution of ERPs to investigate mechanisms underlying age- and performance-related differences in working memory. Young and old subjects participated in a verbal n-back task with three levels of difficulty. Each group was divided into high and low performers based on accuracy under the 2-back condition. Both old subjects and low-performing young subjects exhibited impairments in preliminary mismatch/match detection operations (indexed by the anterior N2 component). This may have undermined the quality of information available for the subsequent decision-making process (indexed by the P3 component), necessitating the appropriation of more resources. Additional anterior and right hemisphere activity was recruited by old subjects. Neural efficiency and the capacity to allocate more resources to decision-making differed between high and low performers in both age groups. Under low demand conditions, high performers executed the task utilizing fewer resources than low performers (indexed by the P3 amplitude). As task requirements increased, high-performing young and old subjects were able to appropriate additional resources to decision-making, whereas their low-performing counterparts allocated fewer resources. Higher task demands increased utilization of processing capacity for operations other than decision-making (e.g., sustained attention) that depend upon a shared pool of limited resources. As demands increased, all groups allocated additional resources to the process of sustaining attention (indexed by the posterior slow wave). Demands appeared to have exceeded capacity in low performers, leading to a reduction of resources available to the decision-making process, which likely contributed to a decline in performance. ■

INTRODUCTION

Understanding age-related changes in working memory (WM) (Smith et al., 2001; Hartley, 1992; Dobbs & Rule, 1989) is critical, given the importance of their contribution to cognitive decline in old age (Oberauer, 2005; Salthouse & Ferrer-Caja, 2003). Old adults often appropriate more resources than young adults to carry out WM tasks, especially under less demanding conditions (Reuter-Lorenz & Sylvester, 2005; Smith et al., 2001; Grady, 2000). For example, in an fMRI study, Mattay et al. (2006) found that on a 1-back task, older subjects performed as well as younger ones, but exhibited greater prefrontal cortical (PFC) activity bilaterally. At higher WM loads, older individuals performed worse than younger ones and exhibited relatively reduced activity in these prefrontal regions. Some researchers also have found that in young subjects, prefrontal activity increases to meet additional processing demands up until the point in which the limits of a person's WM capacity have been reached, at which time neural activity may begin to decrease (Mattay et al., 2006; Callicott et al., 1999; Goldberg et al., 1998).

To account for changes in neural activity associated with both increased task demands and with aging, Reuter-Lorenz and Cappell (2008) have proposed the compensation-related utilization of neural circuits hypothesis, or "CRUNCH" model. It suggests that individuals recruit additional neural activity as task load increases. Due to less efficient processing, older adults rely upon additional neural activity at lower demand levels than younger adults, which is viewed as a compensatory activity for age-related cognitive decline (Schneider-Garces et al., 2010). Beyond a certain level of task demand, the brains of older adults may reach their capacity limits, leading to underrecruitment and a decline in performance relative to young adults. According to the CRUNCH model, differences between old and young adults in the over- and underrecruitment of neural activity may be a function of age-associated differences in processing capacity. CRUNCH suggests that relative task difficulty (reflecting the level of congruency between task demand and WM ability) alone can account for observed age-related differences in activation.

Results in the aging literature often are characterized in terms of how old adults differ from young adults, implying relatively uniform age-related changes. Such characterizations may obscure information about different patterns of normal aging. Recently, there has been increasing interest not only in making overall distinctions between normal and diseased cognitive aging but also in defining sources of individual differences within older populations (Riis

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et al., 2008; Fabiani, Friedman, & Cheng, 1998). Identifying factors that may contribute to the most successful patterns of cognitive aging has become increasingly important as a growing portion of the population is reaching old age (Daffner, 2010).

Particularly pertinent to the current study is the observation that there are substantial differences across individuals in the resources needed to carry out WM tasks. Many functional imaging and ERP studies suggest that high-performing young subjects are able to carry out an experimental task more efficiently than their low-performing counterparts (Smith et al., 2001; Rypma & D'Esposito, 2000; McGarry-Roberts, Stelmack, & Campbell, 1992). For example, P3 latency, a measure of speed of information processing (Polich, 1996; Kutas, McCarthy, & Donchin, 1977), is shorter in individuals with higher intellectual capacity or better performance on attentional tasks, a finding that has been observed among both young and old subjects (Riis et al., 2008; Walhovd & Fjell, 2002; Jausovec & Jausovec, 2000; Polich, Howard, & Starr, 1983). P3 amplitude, a measure of resource allocation (Polich, 1996; Wickens, Kramer, Vanasse, & Donchin, 1983), tends to be lower in young subjects with higher IQ or better neuropsychological performance (Riis et al., 2008; Egan et al., 1994). In contrast, several studies have suggested that older adults who perform better on WM and related tasks allocate more resources than age-matched adults who perform worse (Riis et al., 2008; Daffner et al., 2006; Reuter-Lorenz et al., 2000; Rypma & D'Esposito, 2000). Most studies examining differences between young and old subjects in neural correlates of WM processing have not divided groups into high versus low performers, which we hypothesized would modulate age-related effects. We anticipated that for both young and old subjects, differences between high and low performers in the amount of resources allocated to perform a WM task would vary as a function of task demand.

In the current investigation, ERPs were used as measures of neural activity. In contrast to other functional imaging techniques, ERPs can provide indices not only of resource allocation but also of speed of information processing. Moreover, their excellent temporal resolution offers an opportunity to examine changes in mental operations occurring at different points in the information processing stream. We focused on the cognitive operations indexed by three ERP components—P3, N2, and slow wave—all of which are carried out within the first second after the occurrence of an event.

The P3 component[1] has been conceived as representing the process of categorizing an event (Kok, 2001; Ford, 1978; Squires, Hillyard, & Lindsay, 1973) or updating memory after an event has been categorized (Donchin & Coles, 1988; Donchin, 1981). The amplitude of the P3 component can serve as a measure of the amount of capacity-limited processing resources allocated to carry out decision-making/ updating operations. For example, investigations using dual-task paradigms have demonstrated that as the demands of the primary task are augmented, there is an increase in P3 amplitude to targets in the primary task, consistent with greater allocation of processing resources, and a reciprocal reduction of the P3 amplitude to targets in the secondary task, reflecting capacity limitations and the diminished availability of resources (Sirevaag, Kramer, Coles, & Donchin, 1989; Wickens et al., 1983).

Several studies also have reported a decline in the P3 amplitude in young subjects as WM load increases (Gevins et al., 1996; Mecklinger, Kramer, & Strayer, 1992; Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1992). This decline in P3 amplitude has been interpreted as reflecting the dual-task nature of the *n*-back paradigm, whose execution depends on different sets of operations (Watter, Geffen, & Geffen, 2001; McEvoy, Smith, & Gevins, 1998). According to this hypothesis, one set of operations involves maintenance and manipulation of the contents of WM. Another set of operations, which is indexed by the P3, involves decision-making, in which subjects deliberately determine if the stimulus presented is a target based on whether it matches a designated representation held in WM. Both sets of operations are postulated to be derived from a shared pool of limited resources (McEvoy et al., 1998; Kahneman, 1973).[2] Thus, as the demands of an *n*-back task increase, resources that previously have been devoted to decision-making/ updating are believed to be "reallocated" to the operations of maintenance, manipulation, and sustaining attention, leading to a decline in P3 amplitude to *n*-back targets.

In the current study, young and old subjects participated in a verbal *n*-back task in the visual modality with three levels of difficulty (0-back, 1-back, 2-back). Each group was divided into high and low performers based on accuracy under the 2-back condition. Several major issues were investigated. First, are there age-related differences between high and low performers in the efficiency of WM processing, as measured by the P3 component in response to target *n*-back events? We anticipated that under the easiest condition, the 0-back, high performers in both age groups would exhibit more efficient processing than their low-performing counterparts, as indicated by a smaller, earlier P3 response. We also anticipated that as task demands increased, high performers in both age groups would be able to increase the amount of resources appropriated to decision-making/updating, whereas low performers would either appropriate the same or fewer resources. We expected that the capacity limit would differ between high and low performers (i.e., the level of demand in which P3 amplitude would begin to decrease, rather than increase) and that this result would be modulated by age. Age-related differences in WM performance and resource allocation would be smaller across high than low performers. Consistent with the CRUNCH model (Schneider-Garces et al., 2010; Reuter-Lorenz & Cappell, 2008), we predicted that the more closely WM abilities were aligned in subjects from the old and young age groups, the more closely their pattern of resource-allocation-by-task-load would overlap. Moreover, we speculated that there may be a closer alignment of WM capacity between young and old high-performing

subjects than between high- and low-performing young subjects. Thus, we anticipated that there would be greater similarity in the pattern of P3 amplitude versus WM demand between high-performing young and high-performing old subjects than between high- and low-performing subjects within either age group.

Davis, Dennis, Daselaar, Fleck, and Cabeza (2008), Daselaar and Cabeza (2005), and Cabeza, Anderson, Locantore, and McIntosh (2002) have suggested that compensatory neural activity in older individuals can manifest in several ways, including the development of a more bilateral pattern of frontal activity (labeled the hemispheric asymmetry reduction in old age or "HAROLD" model), or the reduction in posterior activity coupled with an increase in frontal activity (labeled the posterior–anterior shift in aging or "PASA" model). Based on the aging and WM literature (Reuter-Lorenz & Sylvester, 2005; Reuter-Lorenz et al., 2000), we anticipated that older individuals would recruit additional frontal and right hemisphere processors to carry out this experiment's verbal WM task, as measured by changes in the P3 scalp distribution. If age-related differences in the scalp distribution were larger for high- than low-performing old subjects, it would strengthen the thesis that such changes reflect a successful compensatory mechanism.

The second issue involved whether individual and age-related differences in the amount of resources allocated to decision-making (as indexed by the P3) can be explained by differences in operations that occur earlier in the information processing stream. Degradation or delays in earlier processing might undermine the quality of information available to individuals when decisions about targets need to be made (Reuter-Lorenz & Cappell, 2008; Rypma & D'Esposito, 2000). The focus of this study was on the N2 component, which tends to peak around 200 msec earlier than the P3 peak. A recent review of the anterior N2 (N2b) in the visual modality (Folstein & Van Petten, 2008) made a strong case for the idea that the N2b component can be generated by a mismatch between a currently presented stimulus and a representation held in memory. The N2b component also is generated in response to matching events, but is smaller in amplitude than in response to mismatches. Impairment of this earlier mismatch/match process, as measured by the anterior N2b, would likely have an impact on the subsequent decision-making process, as measured by the P3, which determines whether an event is an n-back target. We anticipated that with increasing n-back task demands, the intervening delay between presentation of a stimulus and the representation held in memory would lead to an attenuation of the N2b response. If so, this would place a greater burden on the subsequent decision-making process, indexed by the P3.

Prior research led to the prediction of an age-related reduction of the N2b component (Riis et al., 2008; Muller & Knight, 2002; Snyder & Hillyard, 1979). However, it was less clear whether there would be a difference in N2b amplitude between high- and low-performing old subjects. One possibility was that high-performing old individu-

als would exhibit a more robust N2b response than low-performing old individuals, placing fewer demands on later decision-making processes. An alternative possibility was that there would be little difference between high- and low-performing old individuals in this earlier mismatch/match process. If so, high performers may differ from low performers in their capacity to compensate for these age-related deficits by augmenting later controlled processing.

The third issue involved looking for a potential marker of the hypothesized diversion of resources from decision-making (indexed by the P3) to other operations, as task demands increase. McEvoy et al. (1998) have suggested that as the load of an n-back task goes up, increased demands are made on sustaining attention and maintaining concentration. These functions are conceived of as reflecting a more general cognitive response to increasing difficulty, not linked to the specific task involved. The focus of the current study was on the posterior slow wave, which often is considered to be a marker of sustained attention and effort (Rushby, Barry, & Doherty, 2005; Gevins et al., 1996; Ruchkin, Sutton, Kietzman, & Silver, 1980).[3] The amplitude of the posterior slow wave increases as a function of task demand, even under conditions in which the amplitude of the preceding P3 declines (Ruchkin & Sutton, 1983; Ruchkin et al., 1980).

Assuming that the effort made by subjects to carry out the experimental task was optimal (Gopher, 1984), we expected that under more challenging n-back conditions, all groups would devote additional resources to sustaining attention, that would be indexed by an increase in the amplitude of the posterior slow wave. Low performers, with smaller overall capacity, would likely reach their processing limits under lower n-back task demands. Under such conditions, fewer resources would be available to devote to decision-making. If this hypothesis was correct, we would expect that among low performers, as the demands of the task increased, the size of the posterior slow wave and the size of the P3 would move in opposite directions. A major behavioral consequence of having fewer resources available for the decision-making process would be a decline in accuracy of detecting n-back targets.

Finally, we were mindful of the problems associated with evaluating age-related differences in neural activity when subject groups not only differ in age but also task performance (Rugg & Morcom, 2005). Thus, we sought to identify subsets of individuals from each age group who performed comparably on the n-back tasks. This allowed us to examine age-related differences in cognitive processing, as measured by ERPs, used to carry out the task at similar levels of performance.

METHODS

Participants

Participants were recruited through community announcements, including the Harvard Cooperative Program on Aging.

To be included in the study, participants had to be 18–30 years old (young subjects) or 65–85 years old (old subjects), English-speaking, and have 12 years or more of education. Old subjects had to score 26 or more on the Mini-Mental Status Exam (Folstein, Folstein, & McHugh, 1975). Subjects were excluded if they had a history of central nervous system diseases or major psychiatric disorders based on the DSM-IV criteria (American Psychiatric Association, 1994), a history of clinically significant medical diseases, corrected visual acuity worse than 20/40, or focal abnormalities on neurological examination consistent with a lesion of the central nervous system. Participation was voluntary and subjects were compensated $25 per hour. The study was approved by the Institutional Review Board of Brigham and Women's Hospital, Boston, MA.

All subjects were administered the American Modification of the National Adult Reading Test (AMNART; Ryan & Paolo, 1992), which provides an estimate of IQ. In addition, all participants completed the following standard psychometric tests: (1) Controlled Oral Word Association Test (COWAT; Ivnik, Malec, Smith, Tangalos, & Petersen, 1996); (2) category fluency (animals; Spreen & Strauss, 1998); (3) Visual Form Discrimination Test (Benton, Varney, Hamsher, & Spreen, 1983); and (4) Trail Making Test, Part B (Tombaugh, 2004). Percentile performance on each task was determined based on performance relative to published age-matched norms. A composite percentile performance was computed for each subject based on the mean percentile performance score on the four cognitive tests.

Experimental Tasks

Participants performed a verbal n-back paradigm in the visual modality with three levels of difficulty (0-back, 1-back, 2-back). Stimuli consisted of letters of the alphabet, white on a black background, presented at the center of a high-resolution computer monitor for 200 msec, in pseudo-random order (Figure 1). Under each n-back condition, subjects were shown a series of 300 letters, divided into three blocks. For each level of n-back, 75% of trials were nonmatches and 25% of trials were matches. Subjects were instructed to respond only to match letters (button

press on a game controller). Subjects were told to respond as quickly as possible without sacrificing accuracy. The interval between the onset of consecutive visual stimuli was fixed at 2200 msec. The hand used for button press and the order of n-back level were counterbalanced across subjects.

ERP Recordings

Subjects were fitted with an electrode cap (Electro-Cap International) with 35 tin electrodes. Electrode locations were based on the International 10–20 System and were arranged in five columns (midline [ML], 2 inner lateral [IL], 2 outer lateral [OL]), each with seven anteroposterior sites (Figure 2). All electrodes were referenced to an electrode placed on the left mastoid bone. Additional electrodes were placed under the left eye (referenced to the left mastoid), lateral to the right eye (referenced to an electrode lateral to the left eye), and on the right mastoid bone (referenced to the left mastoid) to monitor for blinks, horizontal eye movements, and asymmetrical mastoid activity. Impedance levels for all electrodes were maintained under 5 kΩ. The EEG was sampled continuously at 200 Hz, amplified by an SA Instruments bio-amplifier system (using a band filter with negative 3-dB cutoffs set at 0.01 and 40 Hz), and sent to an analog–digital converter.

Data Analysis

RT and percent hit rate were measured for match trials. RT was computed as the median duration (msec) between stimulus onset and button press that occurred between 200 and 2400 msec poststimulus onset. Accuracy was defined as percent hits minus percent false alarms. ERPs were recorded and averaged for match and nonmatch trial types separately for each level of n-back. Only trials in which subjects responded correctly were averaged. Trials with horizontal eye movement artifact or amplifier blocking were excluded. A blink correction algorithm, using principal components analysis, was employed that computed the impact of the blink on the waveform in each channel (Dale, 1994). The temporal intervals for ERPs were based on careful

Figure 1. Illustration of the timing of the stimulus presentation under the 2-back condition.
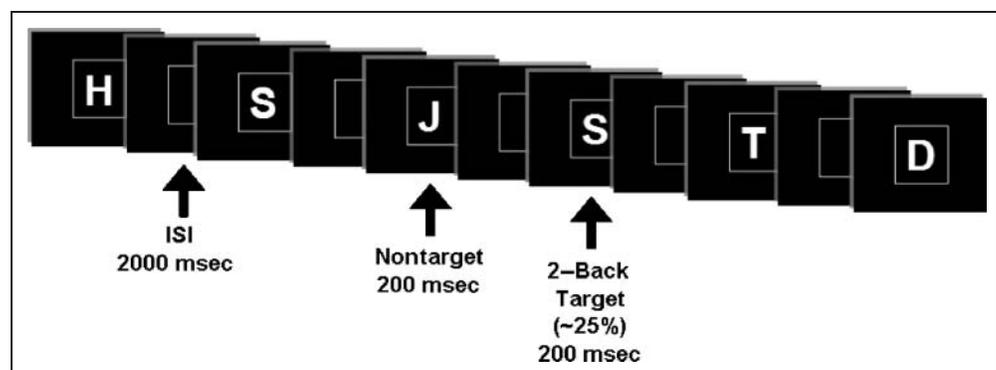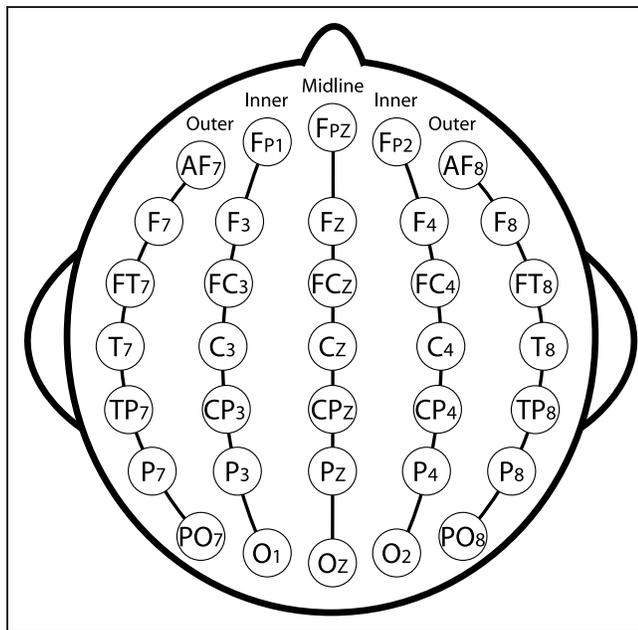
Figure 2. Montage illustrating the location of electrode sites, based on the International 10–20 System, which includes midline, two inner lateral, and two outer lateral columns, each with seven anteroposterior sites.

review of the grand average and individual ERP plots for each subject. The P3 component was defined as the local positive peak 275–650 msec after stimulus onset. The N2 component was defined as the local negative peak 210–350 msec after stimulus onset,[4] and the posterior slow wave was defined as the mean amplitude 700–1000 after stimulus onset. All components were measured with respect to the average of the 100-msec prestimulus baseline. ERP latencies were defined as the time from stimulus onset to the local peak at midline sites.

A repeated measures analysis of variance (ANOVA) was performed on ERP data with age (young, old) and performance (high, low) as between-subjects variables, and n-back level (0-back, 1-back, 2-back) and electrode site as within-subjects variables. Data for all components were analyzed for midline sites. In addition, P3 data were analyzed for lateral sites. Lateral sites were further divided according to inner and outer columns (Figure 2), which are only reported when the information is pertinent to the major issues being addressed. Analyses of scalp distribution using raw data (Urbach & Kutas, 2002) focused on determining whether there were anteroposterior differences or hemispheric differences across subject groups. Analyses that yielded significant interactions between subject group, condition, or electrode site resulted in planned contrasts between the levels of the variable. The Geisser–Greenhouse correction was applied for all repeated measures with greater than 1 degree of freedom.

RESULTS

Participants

Forty-one individuals were included in this study. Data from an additional three old subjects and two young subjects were excluded because of excessive EEG artifact (resulting in <25 artifact-free trials of any stimulus category). Subjects in each age group were divided by a median split into high versus low performers based on ability to discriminate between targets and nontargets (d') under the 2-back condition. The characteristics of the subject groups are summarized in Table 1. Participants were well-educated and had high estimated IQs. There were no group differences in sex or years of education. High performers had higher estimated IQs than low performers. Differences in

Table 1. Subject Characteristics

	Young		Old		Age Effect	Perf. Effect
	High Performers	*Low Performers*	*High Performers*	*Low Performers*		
n	12	11	9	9	✕	✕
Age	22.8 (1.9)	22.3 (2.1)	72.1 (7.6)	73.6 (4.4)	$p < .0001$	ns ($p > .7$)
Sex	7F/5M	8F/3M	6F/3M	7F/2M	ns ($p > .6$)	ns ($p > .4$)
Years of Education	16.3 (1.1)	15.6 (1.5)	17.2 (3.8)	16.3 (3.5)	ns ($p > .3$)	ns ($p > .3$)
MMSE	✕		29.1 (0.9)	29.1 (0.9)	✕	ns ($p = 1.0$)
AMNART Estimated IQ	122.8 (4.6)	118.5 (4.4)	127.2 (4.1)	119.9 (8.9)	ns ($p > .1$)	$p < .005$[a]
Composite percentile performance	69.4 (15.0)	55.6 (19.0)	73.2 (14.0)	57.6 (13.2)	ns ($p > .5$)	$p < .005$[a]

No Age × Performance interactions.

Perf. = performance based on 2-back task accuracy (d′).

Composite percentile performance vs. age-matched norms: Trails Part B, COWAT, Category Generation (Animals), Benton Visual Form Discrimination.

[a]High Performers > Low Performers.

estimated IQ were not modified by age. High performers on the *n*-back task also did better on the neuropsychological tests. Based on age-matched norms, high performers scored in the 71st percentile and low performers in the 57th percentile on the composite of the neuropsychological tests. The difference between high and low performers was not modified by age. The strongest correlation between accuracy on the 2-back task (d') and performance on neuropsychological tests was observed for time to complete Trail Making, Part B ($r = -.76, p < .00001$).

Behavioral Results

Accuracy

The accuracy level of the different subject groups under each of the *n*-back conditions is displayed in Figure 3A. An ANOVA revealed an effect of age [$F(1, 37) = 33.68$, $p < .00001$], performance [$F(1, 37) = 30.81, p < .00001$], and condition [$F(2, 74) = 234.90, p < .00001$], and interactions between age and performance [$F(1, 37) = 6.00$, $p < .05$], age and condition [$F(2, 74) = 26.67, p < .00001$], and performance and condition [$F(2, 74) = 30.84, p < .00001$].

Young subjects were more accurate than old subjects [mean (*SEM*): 94.2% (0.7) vs. 88.0% (0.8)]. High-performing subjects were more accurate than low-performing subjects [94.1% (0.8) vs. 88.1% (0.8)]. Accuracy was higher under the 0-back than the 1-back, which in turn was higher than under the 2-back condition. The interaction between

Figure 3. (A) Accuracy level (% hits − % false alarms) to *n*-back targets under each condition. (B) RT (msec) to *n*-back targets under each condition.

age and performance was present because age-related differences in overall accuracy were smaller for high- than low-performing adults. The interaction between age and condition was present because the decline in accuracy going from 1-back to 2-back was larger for old than young subjects. Similarly, the interaction between performance and condition was due to there being a larger cost going from 1-back to 2-back for low performers than high performers. However, the three-way interaction between condition, age, and performance did not reach significance. It is important to point out that there were no differences between groups in *n*-back accuracy on the 0-back task or 1-back task, but only on the 2-back task. On the 2-back task, high-performing young subjects were more accurate than the other three groups. There was no difference in accuracy between the high-performing old and the low-performing young subjects. Both of these groups were more accurate than low-performing old subjects.

Reaction Time

RT data were not normally distributed. Thus, comparisons of RTs between groups were made after computing the log transformation. An ANOVA revealed an effect of age [$F(1, 37) = 7.69, p < .01$] and condition [$F(2, 74) = 34.14, p < .00001$], no effect of performance, and an interaction between condition and age [$F(2, 74) = 5.17, p < .05$] (see Figure 3B). Old subjects had longer median RTs than young subjects [597 (28) msec vs. 499 (25) msec]. High and low performers did not differ in terms of RTs ($p > .1$). RT to 2-back hits was longer than to 1-back hits, which in turn was longer than to 0-back hits. The interaction between condition and age was a result of the magnitude of the increase in RT in response to higher task demands being larger for old than young subjects. It also reflected the fact that under the 0-back condition there was no effect of age ($p = .1$); under the 1-back, there was a trend ($p < .07$), whereas under the 2-back, young subjects were significantly faster than old subjects ($p < .01$). The interaction between condition and age was not modified by performance.
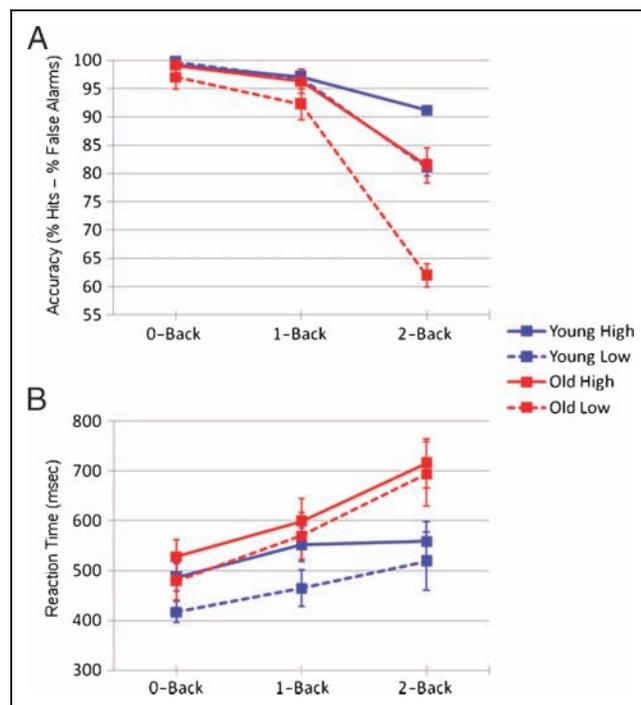
ERPs

N2 Component at Midline Sites for n-Back Target Hits and Nontargets

N2 amplitude. The grand-average ERPs to *n*-back hits at selected midline sites for each subject group under the three *n*-back conditions are illustrated in Figure 4. Because the N2b component is believed to reflect the activity of a match/mismatch process, with a much larger response to mismatches, both *n*-back target hits (matches) and *n*-back nontargets (mismatches) were analyzed. Figure 5 illustrates N2 surface potential maps in response to nontarget (mismatch) events. An ANOVA with age and performance as between-subject variables, and stimulus type (match vs.

Figure 4. Midline grand-average ERP plots of *n*-back hits. Arrows indicate N2, P3, and posterior slow wave components.
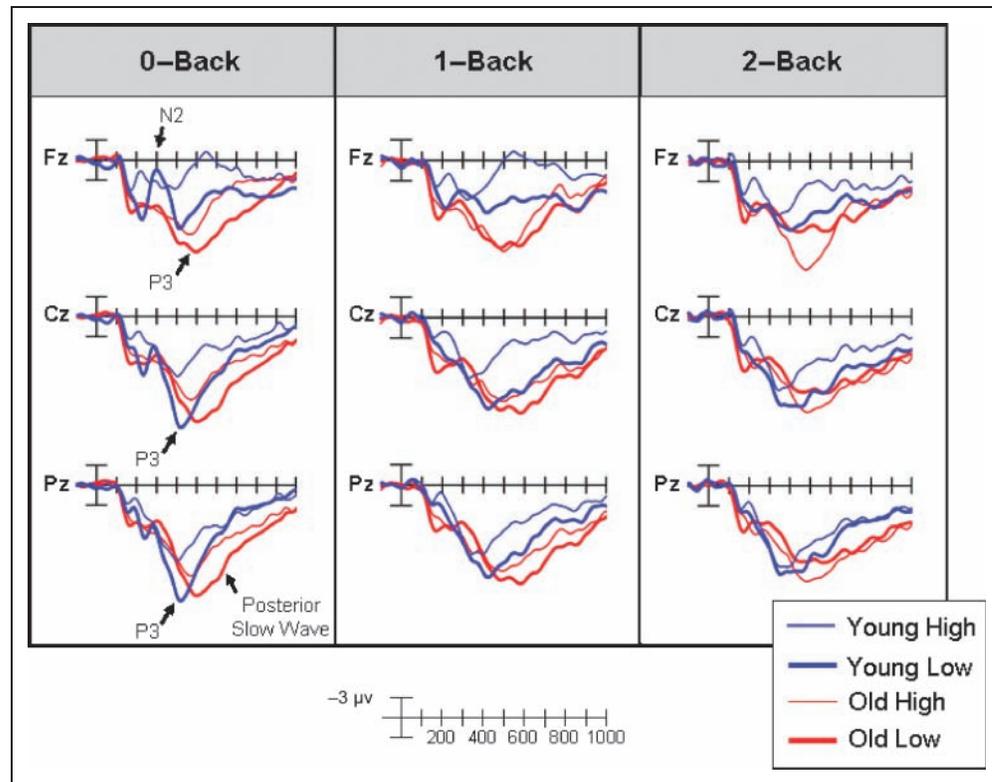
mismatch), condition, and midline sites as within-subject variables was performed. This ANOVA revealed an effect of age [$F(1, 37) = 4.21, p < .05$], stimulus type [$F(1, 37) = 68.52, p < .00001$], and condition [$F(2, 74) = 5.63, p < .01$], but not performance. In addition, there were interactions between stimulus type and site [$F(6, 222) = 19.29, p < .00001$], and between age and site [$F(6, 222) = 4.20, p < .05$]. Young subjects generated a much larger N2 than old subjects. The magnitude of this effect was similar for high- and low-performing subjects. The N2 response to nontargets was much larger than to targets. This effect was not modified by age, performance, or condition. The N2 was larger under the 0-back than the other two conditions. It was numerically larger under the 1-back than the 2-back condition, but this effect was not reliable ($p < .18$). The interaction between stimulus type and site reflected the fact that for nontargets, the N2 amplitude was largest at fronto-central sites [$F(6, 222) = 4.15, p < .05$], whereas for target hits the N2 was more evenly distributed across the scalp [$F(6, 222) = 2.86, p > .05$]. The interaction between age and site was because young subjects generated a more anteriorly distributed N2 than old subjects, with no differences in this pattern between target and nontarget events.

N2 latency. An ANOVA demonstrated an effect of performance [$F(1, 37) = 8.57, p < .01$], condition [$F(2, 74) = 3.28, p < .05$], and stimulus type [$F(1, 37) = 26.45, p < .0001$], and an interaction between age and site [$F(6,$

$222) = 3.88, p < .05$]. In contrast to N2 amplitude in which there were no differences between high and low performers in either age group, N2 latency varied as a function of performance. The N2 latency of high performers was earlier than low performers. This interaction was not modified by age. The N2 latency under the 0-back condition was later than under the other two conditions. The N2 latency in response to *n*-back targets was earlier than to *n*-back nontargets.

P3 Amplitude

P3 surface potential maps for *n*-back hits are illustrated in Figure 6. Figure 7 presents line graphs of the midline P3 amplitude (mean of the 7 midline sites) in response to *n*-back hits across the four subject groups and three conditions. Main effects or interactions that are not pertinent to the major issues of this study will not be addressed.

An ANOVA revealed a trend toward an effect of age [midline (ML): $F(1, 37) = 3.12, p < .09$; lateral (Lat): $F(1, 37) = 3.99, p < .07$], but no effect of condition or of performance. The most salient interactions involved Age × Site [ML: $F(6, 222) = 14.22, p < .00001$; Lat: $F(6, 222) = 15.93, p < .0001$]; Age × Hemisphere [Lat: $F(1, 37) = 4.71, p < .05$; inner lateral (IL): $F(1, 37) = 4.28, p < .05$; outer lateral (OL): $F(1, 37) = 4.05, p = .05$]; Condition × Site at midline locations [ML: $F(12, 444) = 3.25, p < .05$; Lat: $F(12, 444) = 1.60, p < .2$], and Condition × Performance [ML: $F(2, 74) = 7.64, p < .01$; Lat: $F(2, 74) = 6.53, p < .01$]. Old subjects

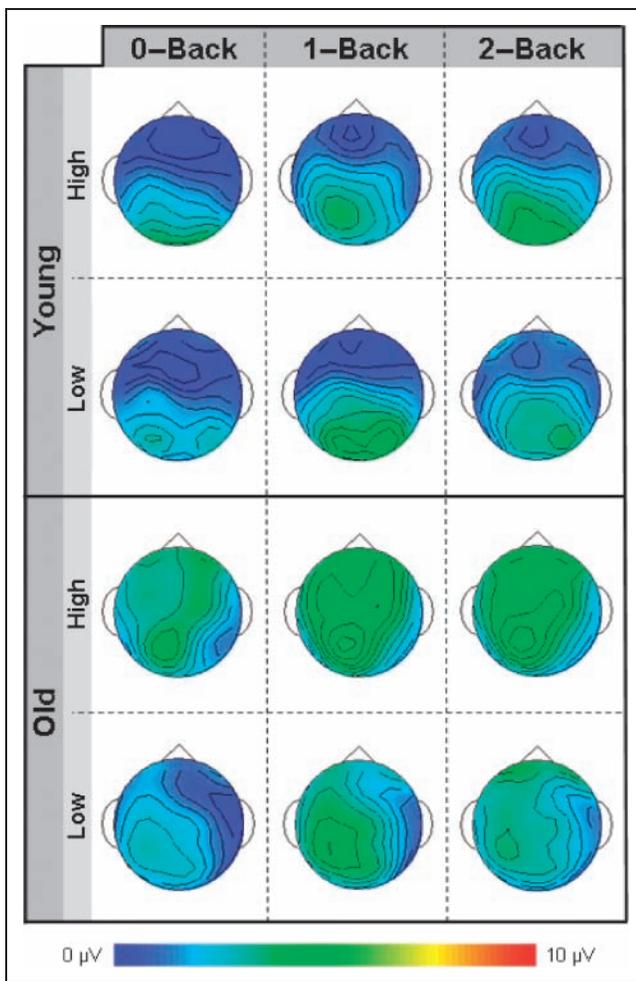**Figure 5.** N2 surface potential maps in response to nontarget (mismatch) events under each condition.
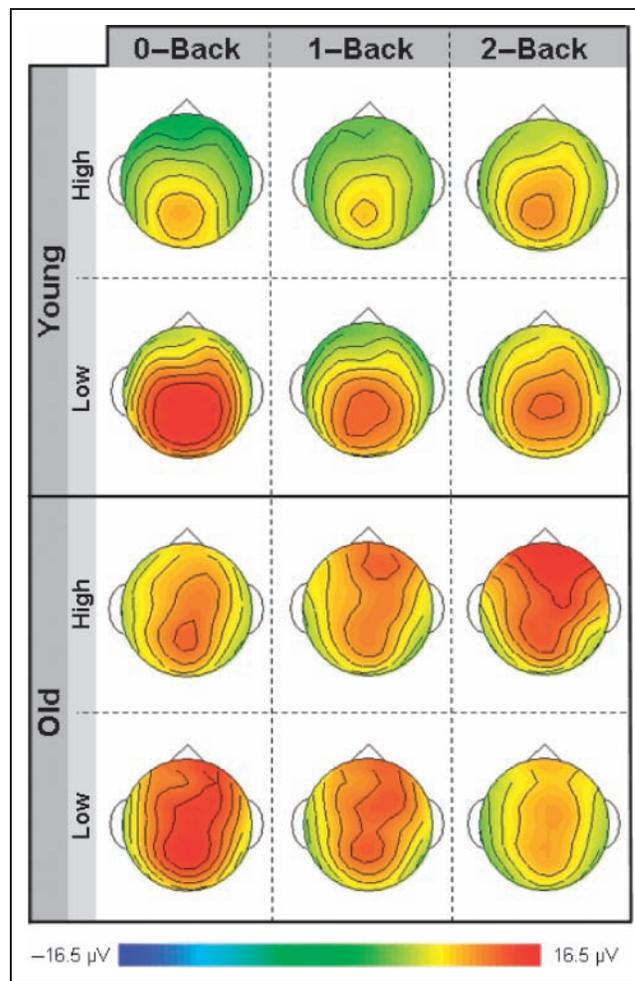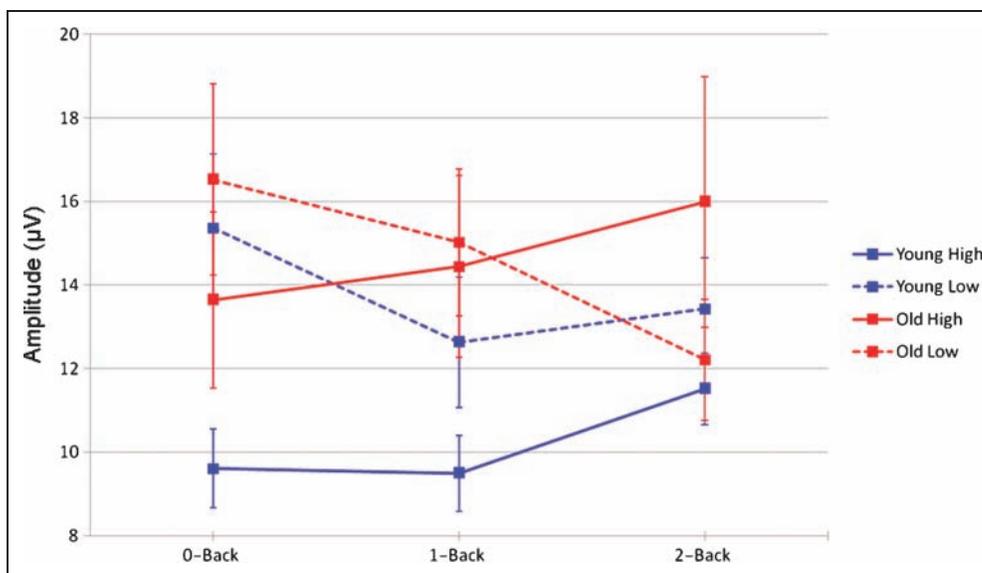

Figure 6. P3 surface potential maps in response to *n*-back hits under each condition.

Figure 7. Line graph illustrating the midline P3 amplitudes (mean of the 7 electrode sites) in response to *n*-back hits under each condition.

tended to exhibit a larger P3 to *n*-back hits than young subjects. The interaction between age and site was present because, at fronto-central sites, the age differences were quite robust. The interaction between age and site also suggested that old subjects generated a more anteriorly distributed P3 than young subjects. This age-related difference in scalp distribution was not modulated by performance.

The interaction between age and hemisphere was present because across left hemisphere sites, there were no age-related differences in the amplitude of the P3, whereas across right hemisphere sites, old subjects generated a larger P3 amplitude than young subjects [effect of age, Lat: $F(1, 37) = 6.23, p < .05$; IL: $F(1, 37) = 4.92, p < .05$; OL: $F(1, 37) = 7.16, p < .05$]. The magnitude of the interaction between age and hemisphere did not differ across *n*-back conditions. Age-related differences in hemispheric scalp distribution were not modulated by performance. The interaction between condition and site was present because as task demands increased, the P3 became more anteriorly distributed. Interestingly, this interaction between site and condition was reliable for young subjects [$F(12, 252) = 2.71, p < .05$], but not old subjects.

One of the most striking findings involved the interaction between condition and performance, which was of similar magnitude for old and young subjects. For high performers, the size of the P3 to target *n*-back events increased as the demands of the task were augmented (2-back > 1-back ≅ 0-back) [ML: $F(2, 38) = 5.13, p < .05$; Lat: $F(2, 38) = 5.54, p < .05$; Figures 5 and 6]. In contrast, for low performers, the magnitude of the P3 to target events decreased as the demands of the task were augmented, especially at midline sites (0-back > 1-back ≅ 2-back) [ML: $F(2, 36) = 3.81, p < .05$; Lat: $F(2, 36) = 2.53, p < .11$; IL: $F(2, 36) = 2.96, p < .08$; OL: $F(2, 36) = 1.88, p < .18$].

In looking at Figure 6, one observes that the lines representing P3 amplitude across the three levels of the *n*-back task move in an upward direction (i.e., increasing amplitude) for high performers, but in a downward direction for low performers. However, there is a noteworthy difference in the pattern of response between old and young subjects. For old subjects, the lines of the high versus low performers actually intersect at the 1-back level, whereas for young subjects the lines never cross, but only come closer to each other at the 2-back condition. Among old subjects, the P3 under the 0-back condition was larger for low than high performers, whereas the P3 under the 2-back condition was larger for the high than the low performers, which resulted in an interaction between performance and condition [ML: $F(2, 32) = 3.66, p < .05$; Lat: $F(2, 32) = 3.42, p = .05$]. In contrast, among young subjects, low performers generated a larger P3 response than high performers under all conditions [effect of condition, ML: $F(1, 21) = 5.37, p < .05$; IL: $F(1, 21) = 4.76, p < .05$; OL: $F(1, 21) = 2.03, p = .17$]. The interaction between performance and condition [ML: $F(2, 42) = 4.15, p < .05$; IL: $F(2, 42) = 3.71, p < .05$; OL: $F(2, 42) = 1.84, p < .18$] was present because the smallest difference in P3 amplitude between the high- and low-performing young subjects was observed under the 2-back condition.

Controlling for Group Differences in "Baseline" P3 Amplitude under the Minimal Load Condition

When examining changes in resource allocation associated with increasing WM demands, baseline differences across individuals and groups under the minimal load (0-back) condition need to be taken into account. The use of a repeated measures ANOVA partially addressed this concern, as each participant serves as his or her own "within-subject" control. To further deal with this issue, P3 values for each subject at each midline site under the 1-back and 2-back conditions were recalculated after subtracting the P3 values under the 0-back condition. There was a robust effect of performance [$F(1, 37) = 12.41, p < .01$] and interaction between performance and condition [$F(2, 74) = 7.65, p < .01$]. These results were present because with increasing WM load, the P3 amplitude relative to the 0-back condition got larger for high performers [effect of condition, $F(2, 38) = 5.13, p < .05$], but got smaller for low performers [$F(2, 36) = 3.82, p < .05$]. These results confirm those of the original analysis.

P3 Latency to n-Back Hits

An ANOVA demonstrated an effect of age [$F(1, 37) = 15.90, p < .001$], performance [$F(1, 37) = 4.69, p < .05$], and a strong trend for condition [$F(2, 74) = 3.18, p = .05$]. Interactions were found for Age × Site [$F(6, 222) = 4.25, p < .05$], Performance × Site [$F(6, 222) = 3.27, p < .05$], and Age × Condition [$F(2, 222) = 4.25, p < .05$]. P3 latency was shorter for young than old subjects [409 (12) msec vs. 478 (13) msec]. The magnitude of the age-related increase in P3 latency was as large for high as for low performers. The interaction between age and site was present because the difference between young and old subjects was observed at all midline sites except FPz. P3 latency was shorter for high performers than low performers [425 (12) msec vs. 462 (12) msec]. The interaction between performance and site reflected the fact that the largest difference in P3 latency was found at frontal sites. The strong trend toward an effect of condition was present because P3 latency under the 0-back condition was shorter than under the 2-back condition and tended to be shorter than under the 1-back condition. The interaction between age and condition was present because for old subjects, the P3 latency increased with greater WM demands (0-back < 1-back ≅ 2-back) [effect of condition, $F(2, 96) = 5.77, p < .01$], whereas for young subjects there were no differences in P3 latency across conditions.

Posterior Slow Wave Activity

Positive slow wave activity was largest at central–parietal sites [main effect of site, $F(6, 222) = 12.87, p < .0001$]

(Figure 4). This effect was not modified by age or performance. Therefore, analyses focused on Cz–Pz electrode sites. [The scalp distribution of the slow wave component differed from that of the P3 component (ERP component type × Site interaction) for both old subjects ($F(6, 96)$ = 5.39, $p < .05$) and young subjects ($F(6, 126) = 12.71$, $p < .0001$). For old subjects, the slow wave was more posteriorly distributed than the P3, whereas for the young subjects, the P3 was more posteriorly distributed than the slow wave.] An ANOVA revealed an effect of age [$F(1, 37) = 14.81$, $p < .001$] and condition [$F(2, 74) = 15.43$, $p < .00001$], but not performance (Figure 8). Old subjects generated a larger posterior slow wave than young subjects [7.14 (0.60) µV vs. 4.07 (0.53) µV]. The mean amplitude of the posterior slow wave increased as a function of task demand with significant differences between every n-back level [0-back: 4.41 (0.45) µV; 1-back: 5.44 (0.37) µV; 2-back: 7.00 (0.60) µV]. Most importantly, the effect of condition was not modified by performance or age.

Controlling for Potential Effects of Performance Differences on ERP Results

Confounding age and performance may be particularly problematic when trying to assess between-group differences in neural activity (Rugg & Morcom, 2005). This issue was minimized under the 0-back and 1-back conditions, where accuracy rates largely overlapped and group differences in RT values were either not significant (0-back) or only marginally so (1-back). However, the accuracy of two of the low-performing old subjects was more than 1.75 standard deviations below the mean accuracy for all subjects on the 0-back task. Excluding these two subjects brought the accuracy of the low-performing old subjects more closely aligned with the other groups on the 0-back

and 1-back tasks. Re-running the analyses for the P3 component after excluding these two subjects did not alter the pattern of results for the P3 amplitude.

High-performing Old vs. Low-performing Young Subjects

High-performing old and low-performing young subjects did not differ in overall n-back target accuracy ($p > .8$). Moreover, decline in accuracy as WM load increased was of very similar magnitude for both groups ($p > .8$, see overlapping lines; Figure 3). Low-performing young subjects generated faster RTs than high-performing old subjects [$F(1, 18) = 9.67$, $p < .01$], which was of similar magnitude across n-back conditions. The two groups did not differ in overall P3 amplitude (no effect of group). The interaction between group and site [ML: $F(6, 216) = 6.62$, $p < .01$] was present because high-performing old subjects generated a more anteriorly distributed P3 than low-performing young subjects. There was a trend toward an interaction between group and condition [$F(2, 36) = 2.96$, $p < .07$] that was due to high-performing old subjects exhibiting an increase in P3 amplitude and low-performing young subjects exhibiting a decrease in P3 amplitude as a function of increasing n-back demand. There was no overall difference in P3 latency between groups.

In response to nontarget events, low-performing young subjects generated a larger N2 response than high-performing old subjects [$F(1, 18) = 5.09$, $p < .05$]. However, there was no difference between groups in N2 latency. In response to target events, the N2 amplitude did not differ between groups. N2 latency was earlier for old than young subjects at anterior sites, and young than old subjects at posterior sites [Group × Site interaction, $F(6, 108) = 8.02$, $p < .001$]. Finally, there was a weak tendency for high-performing old subjects to generate a larger posterior slow wave response than low-performing young subjects [$F(1, 18) = 2.90$,

Figure 8. Line graph illustrating the mean posterior slow wave amplitudes at Cz–Pz electrode sites under each condition.
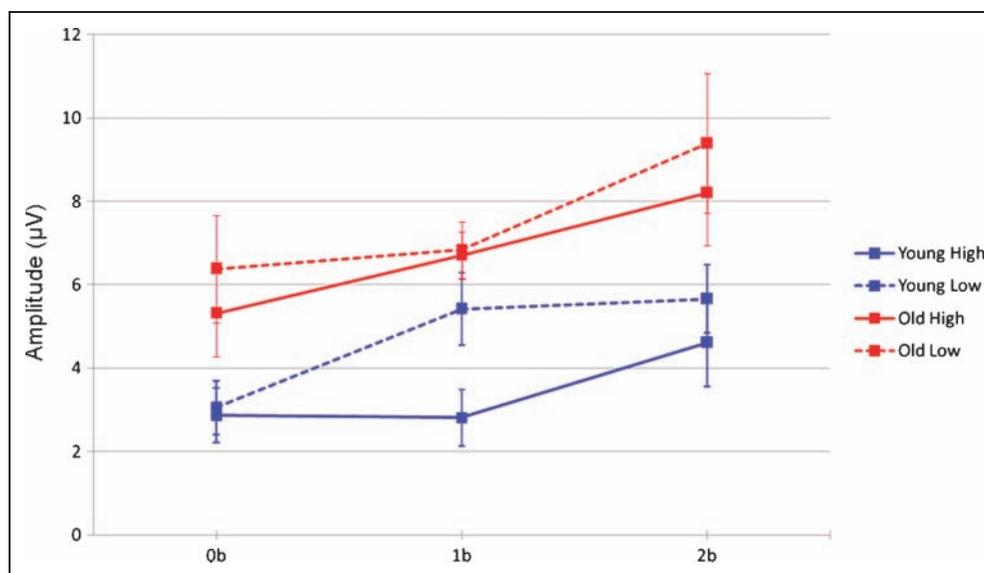
$p < .11$]. There were no interactions between group and condition or site.

Top Half of the High-performing Old vs. Bottom Half of the High-performing Young

As an exploratory analysis, we further divided the high-performing subjects into high–high and low–high performers based on accuracy under the 2-back condition. Young high–high subjects performed more accurately than young low–high subjects and old high–high subjects, with no differences between the latter two groups; old low–high subjects were less accurate than all of the other groups [effect of group, $F(3, 17) = 23.71, p < .00001$]. Because old high–high and young low–high subjects exhibited comparable accuracy overall ($p > .9$), including on the 2-back task ($p > .26$), subsequent analyses focused on these groups. Old high–high subjects had slower RTs than young low–high subjects, with the magnitude of the difference being largest under the 2-back condition [Group × Condition, $F(2, 18) = 4.52, p < .05$]. Overall P3 amplitude did not differ between these two groups [effect of group, $F(1, 9) < 1$, Group × Condition, $F(2, 18) < 1$]. However, there was a Group × Site interaction [$F(6, 54) = 5.10, p < .05$]. The old high–high subjects generated a more anteriorly distributed P3 than the young low–high subjects, an effect that was not modified by condition. P3 latency was earlier for the young low–high than the old high–high subjects [effect of group, $F(1, 9) = 10.82, p < .01$]. The interaction between group and condition [$F(2, 18) = 4.91, p < .05$] was present because the magnitude of the difference was largest under the 2-back.

In response to nontarget events, young low–high subjects tended to generate a larger N2 amplitude than old high–high subjects [$F(1, 9) = 4.11, p < .08$]. However, there was no difference between groups in N2 latency. In response to target events, the N2 amplitude did not differ between groups. The Group × Condition interaction for N2 latency [$F(2, 18) = 6.49, p < .01$] was present because the young low–high subjects generated an earlier N2 under the 2-back condition, but not the other conditions. Finally, there was a strong tendency for old high–high subjects to generate a larger posterior slow wave than young low–high subjects [$F(1, 9) = 4.89, p < .06$].

DISCUSSION

The central goal of this study was to investigate mechanisms underlying age- and performance-related differences in WM. The major findings and conclusions of the study can be summarized as follows: Both old subjects and low-performing young subjects exhibited deficits in preliminary mismatch/match detection operations (indexed by the anterior N2 component), with old subjects generating a smaller anterior N2 component than young subjects, and low-performing young subjects generating a more delayed peak N2 response than high-performing young subjects.

Such deficits may have placed a greater burden on the subsequent decision-making process (indexed by the P3 component), requiring the allocation of supplemental resources to be accomplished.

Compared to young subjects, old subjects recruited additional anterior and right hemisphere activity to manage the decision-making process. High and low performers differed in neural efficiency and the capacity to appropriate extra resources to decision-making in response to greater task demands. Under low demand conditions, high performers could carry out the task by utilizing fewer resources than low performers (as indexed by the P3 amplitude). High-performing young and old subjects were able to allocate additional resources to decision-making as task demands increased, whereas low performers ended up appropriating fewer resources. Augmented task demands likely increased deployment of processing capacity for operations other than decision-making (e.g., sustained attention) that are derived from a shared pool of limited resources. As task demands increased, all groups appropriated additional resources to the process of sustaining attention (as indexed by the posterior slow wave). Among low performers, demands may have exceeded capacity, leading to a reduction of resources available to the decision-making process, as reflected in a diminution of P3 amplitude. The mismatch between task demands and available resources for decision-making likely contributed to a decline in their performance. Evidence for each of these observations will be reviewed below.

Participants

The different groups of subjects in this study were well-matched demographically. Old and young subjects did not differ in years of education, sex, estimated IQ, or percentile performance on neuropsychological tests (based on age-appropriate norms). Each age group was divided by median split into high and low performers based on accuracy on the 2-back task. Of note, the low performers in this sample were well-educated and had above-average intelligence. In future studies, it would be informative to include neuropsychological measures of WM capacity (Brumback, Low, Gratton, & Fabiani, 2005). Such information could help determine the extent to which performance on the experimental n-back task corresponds to standard assessments of WM, and could provide another method for dividing subject groups. Although the current study did not include an independent measure of WM capacity, subjects who exhibited better attentional control, as measured by Trail Making, Part B, were the most accurate on the 2-back task. High-performing subjects also scored much higher on the composite of all four neuropsychological tests, indicating that the differences between groups extend beyond performance on the experimental task. Low performers scored in the average range on neuropsychological tests, whereas high performers scored in the top third relative to age-matched norms.

Behavior

Our prediction that age-related changes in WM decline would be smaller among high performers received partial support, as reflected by the significant interaction between age and performance in overall accuracy. However, age-associated decline in accuracy as a function of increased WM demand was not modified by performance. Consistent with the literature on aging, young subjects had faster RTs than old subjects (Salthouse, 1996). However, this difference was only robust under the 2-back condition. No differences were found between high and low performers in RT, which argues against the superior accuracy among high performers, reflecting a tradeoff between speed and accuracy. Particularly important is that the accuracy rate and, to a lesser extent, RT was similar for all of the groups under the 0-back and 1-back conditions. This means that differences between the groups in ERP response under these conditions cannot be attributed to differences in performance (Rugg & Morcom, 2005). Rather, they are a reflection of the different ways in which the groups process information to generate similar behavioral responses. As discussed below, there also were no differences in performance accuracy between either high-performing old subjects and low-performing young subjects, or between high–high performing old subjects and low–high performing young subjects.

P3 Component

Our prediction that, under the 0-back condition, high performers would exhibit a more efficient decision-making process than low performers was confirmed. To achieve the same level of accuracy in response to 0-back targets, high performers allocated fewer resources and completed cognitive operations in less time than low performers, as indexed by a smaller amplitude, earlier peaking P3 component. These differences between high and low performers were observed for both young and old subjects. As WM demands increased, high performers had the capacity to appropriate additional resources to decision-making/updating, whereas low performers allocated fewer resources. Presumably, the mismatch between available resources and level of task demand manifested as a decline in performance, which was observed.[5]

Robust age-related differences were found in the scalp distribution of the P3 component. Old subjects generated a larger response at anterior sites than young subjects, consistent with the posterior–anterior shift in aging (PASA) hypothesis (Davis et al., 2008), suggesting that they depend more heavily on frontal processors to execute the task. Similarly, old subjects generated larger P3 responses over right hemisphere locations than young subjects, whereas there were no age-related differences in overall amplitude over left hemisphere sites. These results are in keeping with the hemispheric asymmetry reduction in old age (HAROLD) model (Daselaar & Cabeza, 2005) and with pre-

vious studies that have found that old subjects recruit right hemisphere processors to carry out verbal tasks that are managed by young subjects by more selectively recruiting left hemisphere processors (Daselaar & Cabeza, 2005; Reuter-Lorenz & Sylvester, 2005; Reuter-Lorenz et al., 2000). Of note, the age-related differences in P3 scalp distribution (more anterior, more right-sided among old subjects) were not modified by WM load. This result suggests that even under fairly easy conditions, the relative contributions from neural processors used to execute the task may differ between old and young subjects, which is consistent with findings that have been reported in the functional imaging literature (Mattay et al., 2006; Reuter-Lorenz & Sylvester, 2005). For example, Reuter-Lorenz and Sylvester (2005) have found that old individuals tend to activate dorsolateral PFC to execute simple WM maintenance/storage operations that in young individuals tend to only activate ventral lateral PFC and posterior parietal regions. The neural basis for age-related changes in WM has been postulated to reflect alterations in PFC, white matter tracks, and specific neurotransmitter systems such as dopamine (Charlton et al., 2006; Mattay et al., 2006; Raz, Gunning-Dixon, Head, Dupuis, & Acker, 1998).

Several additional points should be noted. First, no differences in P3 scalp distribution were observed between high- and low-performing old subjects. Thus, what distinguishes between the processing activity of high- and low-performing old subjects in this task may not be the networks upon which they rely on, but on how efficiently they utilize them. These results are in keeping with previous findings about the similarity of P3 scalp distribution to novel and target events among old subjects who differed in cognitive status (Riis et al., 2008). A second point is that for young subjects, as task demands increased, the P3 to targets became more anteriorly distributed, which suggests that one way in which young subjects manage increased WM load is by recruiting additional frontal processors (Rypma & D'Esposito, 1999; Klingberg, O'Sullivan, & Roland, 1997), a mechanism that may be employed by older subjects even at low levels of demand (Reuter-Lorenz & Sylvester, 2005; Grady, 2000). These results are in keeping with the CRUNCH model of cognitive aging (Schneider-Garces et al., 2010; Reuter-Lorenz & Cappell, 2008).

Also consistent with the CRUNCH model is the observation that differences between subjects in P3 amplitude across n-back levels were more of a function of WM ability than of age per se. High-performing subjects in both the old and young age groups exhibited increased appropriation of resources as task demands increase, whereas low-performing subjects in both the old and young age groups exhibited a reduction in resources appropriated as a function of increased task demand. These differences between high- and low-performing subjects in the pattern of resource-allocation-by-task-load were not modified by age. Of note, even among high performers, old subjects tended to appropriate more resources, as indexed by P3 amplitude, than did young subjects at each level of the

task. Thus, it seems likely that high-performing old subjects, who carry out the task requirements less efficiently than high-performing young subjects, will reach their capacity limits earlier. As such, we would predict that the pattern of resource-allocation-by-task-load would diverge for old and young high-performing subjects as the task demands were increased further. For example, high-performing old subjects may begin to exhibit a decline in P3 amplitude under a 3-back condition, whereas high-performing young subjects may not do so until executing a 4-back task.

What are potential sources of the different patterns of resource utilization that were observed in the current investigation? Our study took advantage of the excellent temporal resolution of ERPs, inaccessible to most functional imaging techniques. It allowed us to identify and measure several different cognitive operations occurring under 1 sec that may contribute to the age- and performance-related differences observed in WM. We focused on preliminary mismatch/match operations, indexed by the anterior N2, and the process of sustaining attention, indexed by posterior slow wave activity.

N2 Component

We hypothesized that degradation or delays in earlier processing may interfere with the quality of information available when decisions/updating about targets must be made. In the visual modality, the anterior N2 (N2b) is very sensitive to a mismatch or conflict between a presented stimulus and a representation being held in memory[6] (Folstein & Van Petten, 2008; Wang et al., 2003; Kotchoubey, Jordan, Grozinger, Westphal, & Kornhuber, 1996). Consistent with this formulation, the anterior N2 to mismatch (nontargets) was much larger than to *n*-back targets for both young and old subjects. The N2 to matching events (targets) was less anteriorly distributed than to nonmatching stimuli. In fact, the size of the N2 match response was evenly distributed across midline sites. This finding raises the possibility that the N2 response to match events reflected contributions from the N2c as well as the N2b components. The N2c tends to have a posterior (lateral) scalp distribution, and is believed to represent a preliminary categorization process that marks an event as a target (Folstein & Van Petten, 2008; Pritchard, Shappell, & Brandt, 1991; Breton, Ritter, Simson, & Vaughan, 1988; Lovrich, Simson, Vaughan, & Ritter, 1986).

The most pertinent finding was the markedly attenuated anterior N2 response among old subjects. This result is unlikely to simply be the consequence of an overlap between N2 and P3 components, the latter of which was more anteriorly distributed in old subjects. If this were the case, one would expect that the prominent differences in P3 amplitude between high- and low-performing old subjects would have had a dramatic impact on the N2 component. However, the two groups of old subjects did not differ in N2 amplitude. The failure of old adults to generate a robust preliminary electrophysiological signal about

whether a stimulus is a mismatch/match is likely to place a greater burden on the subsequent deliberate decision-making process, which then may require additional resources to be carried out. Consistent with this hypothesis is the age-related increase in the size of the P3 component, especially at anterior sites. Also of note, within each age group, the latency of the N2 response was prolonged among low performers. A potential consequence of this delay in the preliminary mismatch/match process is that even under easy WM conditions, low performers may need to appropriate additional resources to subsequent processing stages, as suggested by a larger P3 amplitude under the 0-back condition. This makes low performers vulnerable to more quickly reaching the limits of their capacity as demands are increased further. An age-related reduction of the anterior N2 component also has been reported in response to novel visual stimuli (Riis et al., 2008, 2009). In addition, age-associated decline in anterior negativity has been observed under conditions in which subjects process conflicting or incompatible representations of perceptual stimuli or motor programs, or deal with a mismatch between expectations and behavioral outcomes (Willemssen, Falkenstein, Schwarz, Müller, & Beste, 2011; Beste, Willemssen, Saft, & Falkenstein, 2009; Mathewson, Dywan, Snyder, Tays, & Segalowitz, 2008; Themanson, Hillman, & Curtin, 2006). These operations are believed to depend on the activity of anterior cingulate cortex (ACC) or its connections. Whether the mismatch and novelty N2 are also mediated by ACC remains to be determined (Folstein & Van Petten, 2008). Interestingly, although ACC does not exhibit significant age-related cortical thinning (Fjell et al., 2009), it undergoes a reduction in tissue integrity (Salat et al., 2009) and functional activity (Vaidya, Paradiso, Boles Ponto, McCormick, & Robinson, 2007; Schultz et al., 1999), which tempts one to speculate that this may contribute to the age-related changes in the anterior N2 and the processes indexed by it.

Posterior Slow Wave Activity

As task demands increased, the P3 response of high- and low-performing subjects exhibited the opposite pattern, whereas the change in posterior slow wave activity was similar across all subject groups—its amplitude increased as a function of increasing task demand. Thus, for low performers, the amplitude of the P3 component and the posterior slow wave moved in opposite directions, whereas for high performers, the size of the two components moved in the same direction. We had hypothesized that: (1) operations involved in sustaining attention and in decision-making/updating are derived from an overlapping pool of capacity-limited processing resources, and (2) low performers reach their capacity limits at lower levels of task demand, which prevents them from being able to allocate additional resources to all of the pertinent operations. It follows that once capacity is reached, as low performers appropriate more resources to sustaining attention (as

indexed by the increased posterior slow wave activity), fewer resources may be available to devote to decision-making/updating (as indexed by a decline in P3 amplitude to targets). Of course, our results do not explain how the brain determines which cognitive operations have a higher priority than others when it comes to allocating limited resources. In this experiment, it appears that operations involved in sustaining attention may trump those involved in decision-making/updating. Perhaps, sustaining attention is prioritized because it provides the necessary conditions under which specific task operations such as decision-making/ updating can take place (Mesulam, 2000).

One concern about our interpretation of these results involves the potential temporal overlap between the P3 and slow wave components. We tried to reduce the likelihood of overlap by choosing a measurement interval for the slow wave (700–1000 msec) that was hundreds of milliseconds later than the local P3 peak measured for all subject groups. However, one could still contend, for example, that the reduced P3 amplitude among low performers under more demanding conditions reflects an increase in trial-to-trial variability in the timing of the P3 peak. Delayed P3 peaks may result in additional positivity being measured as part of the subsequent positive slow wave. Against this possibility is the finding that the pattern of results was the same for P3 peak and P3 mean amplitude (see footnote 4). Trial-to-trial peak variability has less of an impact on measurement of mean than peak amplitude (Luck, 2005). In addition, increased temporal overlap between P3 and the subsequent posterior slow wave would tend to diminish the pattern observed with increasing task demand, where the size of the two components moved in opposite directions for low-performing subjects (Ruchkin & Sutton, 1983). Finally, against the notion that the P3 and slow wave reflect a single overlapping ERP component is the observation that for both old and young subjects the scalp distribution of the P3 component differed from that of the slow wave activity.

Old High–High Performers vs. Young Low–High Performers

The old high–high performers likely represent the most cognitively able older adults. Despite being 50 years more senior than the young low–high group, they were as accurate on the tasks, even under the challenging 2-back condition. Overall P3 amplitude did not differ between these groups, suggesting that they carried out the *n*-back tasks by appropriating similar amounts of processing resources. However, as with all of the old subjects, the old high–high group generated a more anteriorly distributed P3 to *n*-back hits than did the young low–high group, indicating different contributions from anterior and posterior processors. Even when only considering these cognitively very competent old subjects, they seem disadvantaged relative to their younger counterparts in terms of processing speed. Theories about age-related changes in resource utilization based on functional neuroimaging measures may need further modification to account for differences in the speed at which WM operations can be executed. For example, young low–high subjects generated earlier peak N2 and peak P3 latencies in response to targets, and exhibited faster RTs than old high–high subjects. Young low–high subjects also had a more robust preliminary mismatch/match response, as measured by a larger N2 to nontarget stimuli, which, as suggested earlier, may have placed fewer demands upon the subsequent decision-making process. In contrast, old high–high subjects tended to generate larger posterior slow wave activity, suggestive of a need to appropriate more resources to sustain attention to carry out the task. This likely puts the old high–high subjects at risk for reaching their capacity limits at lower levels of demand than young low–high subjects.

Conclusion

In conclusion, this study utilized the subsecond temporal resolution of ERPs to examine processes mediating individual and age-related differences in WM. Preliminary mismatch/match operations (indexed by the anterior N2) and capacity-limited sustained attention (indexed by posterior slow wave activity) influenced the pattern of resource allocation for decision-making/updating (indexed by the P3) that was observed across groups differing in age and performance. Additional research is needed to explore individual differences in the neuroanatomical networks subserving these operations and the changes they may undergo with age.

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Notes

1.   In this article, we have elected not to use the term P3b to describe the P3 response to target *n*-back events. The P3b component is most often viewed as a posteriorly distributed P3 response and the P3a component as an anteriorly distributed P3 response. One of the most commonly observed age-related changes in the P3 response to targets is an anterior shift in scalp distribution. There are several hypotheses regarding the source of this age-related change. We favor the view that this age-associated change reflects increased recruitment of anterior processors to carry out the task. As will be reviewed, we also found a similar anterior shift among young subjects in response to increased *n*-back difficulty. Alternative explanations for the age-related anterior shift in P3 to targets include a reduced ability of older subjects to maintain a mental template of the target which, when presented, is more surprising or unexpected, and thus, also elicits an anteriorly distributed P3a response, or a failure of older subjects to habituate an orienting response (indexed by the anterior P3a) to repeated presentations of target stimuli. Our study was not designed to address the mechanisms that underlie the age-related shift in P3 scalp distribution. Thus, rather than label the P3 in terms of P3b or P3a, we describe its scalp distribution as a function of age or task difficulty.

2. Following a long tradition in experimental psychology and consistent with many of the researchers cited in this article, we have adopted the term "processing resources" to suggest that brains have limited capacity to carry out certain kinds of mental operations or cognitive tasks. Functions that seem to depend on a shared pool of resources include maintaining and manipulating the contents of working memory, sustaining attention, and executing attentional control over dual tasks or over complex operations within a single task. Limitations on processing resources have been inferred by behavioral measures (RT, accuracy) that change as a function of a second task, or by increasing the demands of a single task (Salthouse, 1988). Processing resources and neural activity can be more directly assessed via measures of cerebral blood flow or metabolic activity, or by ERPs such as P3 amplitude. Individuals are likely to vary in capacity (maximum level of demand that can be handled) and efficiency (amount of task-related activity as a function of performance or task load; Stern, 2009). We acknowledge that the notion of a single pool of capacity-limited processing resources is an oversimplification, and there are likely to be multiple pools of limited resources that reflect the activity of different neurocognitive networks. However, certain anatomical nodes are shared by a variety of large-scale networks that mediate different cognitive operations. For example, posterior parietal cortex plays an important role in operations involved in directed attention (Mesulam, 2000; McEvoy et al., 1998), WM (Owen, McMillan, Laird, & Bullmore, 2005), and decision-making/updating (Knight, 1997). Recruitment of this node in the service of one neurocognitive network likely places limits on the capacity for it to be simultaneously recruited for other neurocognitive activities.

3. Because the posterior slow wave amplitude has been found to increase with WM load, one possibility is that it reflects storage or rehearsal aspects of WM (Ruchkin, Johnson, Canoune, & Ritter, 1990; Kok & de Jong, 1980). Against this hypothesis are findings of a common scalp distribution of slow waves in response to spatial and verbal WM tasks, suggesting they do not reflect modality-specific storage of representations, although they could be linked to a more general process that allows for the persistence of information in WM (Gevins et al., 1996). If it turned out that posterior slow wave activity is an index of storage or rehearsal aspects of WM, it would not undermine the major conclusions of the study that emphasize different patterns for P3 and posterior slow wave amplitude across groups as task demands increase.

4. For both P3 and N2 components, ERP data were also examined using the mean amplitude of the 80-msec interval centered at the mean midline local peak latency of a subject's group. The pattern of results for the mean amplitude analyses was very similar to that of the local peak amplitude.

5. An alternative account of the functional significance of the P3 amplitude is that it reflects the amount of information transferred (or the amount of uncertainty that is reduced) (Johnson, 1986; Ruchkin et al., 1980), and not the amount of resources allocated. According to this view, the lower P3 amplitude associated with higher WM demands represents reduced information transfer, which also is reflected in a decline in behavioral performance. However, this framework does not appear to provide an adequate account of the data. Under the 0-back condition, target accuracy and RTs were similar across subject groups. However, low performing subjects generated a larger P3 amplitude than high performing subjects. It seems very unlikely that the larger P3 amplitude under the 0-back condition reflects a process in which low performers had a greater reduction of uncertainty or increase in information transfer than high performers. Moreover, for all groups, performance was worse under the 2-back condition than under the 0-back condition. However, subjects designated as high performers, based on accuracy under the 2-back condition, generated a larger P3 component under the 2-back than the 0-back condition. It seems implausible that, given the decline in performance (accuracy/speed) as WM load increased from the 0-back to the 2-back condition, the growth in P3 amplitude observed represents a larger reduction of uncertainty. Following this logic, it would not make sense to assume that the reduction in P3 amplitude exhibited by low-performing subjects represents a decline in information transfer rather than a reduction in the amount of resources available to be allocated.

6. We have interpreted the anterior N2 as serving to index a nonmatch/match process. Of note, nonmatch trials also required subjects to withhold responses. Another anterior N2 component has been identified which is sensitive to cognitive control processes involving response inhibition and the monitoring of response conflict and performance (Folstein & Van Petten, 2008). Thus, an alternative explanation for the anterior N2 observed in the current study is that it reflects a no-go (cognitive control) anterior N2 component. There are several reasons why we do not favor the cognitive control interpretation of our anterior N2 findings. First, the main effects of age and of condition were not modulated by stimulus type (i.e., the magnitude of the effects were as large for match as nonmatch trials). Second, there is evidence that subjects who exhibit greater cognitive control generate a larger no-go N2 component. However, our study found no difference in the size of the anterior N2 between the high- and low-performing subjects in either age group. Finally, we found the anterior N2 to be smaller under more difficult *n*-back conditions, which theoretically would call on even greater cognitive control mechanisms.

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