

## Use it or lose it? SES mitigates age-related decline in a recency/recognition task

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### Abstract

An important goal of aging research is to determine factors leading to individual differences that might compensate for some of the deleterious effects of aging on cognition. To determine whether socio-economic status (SES) plays a role in mitigating age-related decrements in the recollection of contextual details, we categorized older participants into low- and high-SES groups. Event-related potentials (ERPs) and behavioral data were recorded in a picture memory task involving recency and recognition judgments. Young, old-low and old-high SES groups did not differ in recognition performance. However, on recency judgments, old-low subjects performed at chance, whereas old-high subjects did not differ significantly from young adults. Consistent with their preserved recency performance, a long-duration frontal negativity was significantly larger for recency compared to recognition trials in the ERPs of the old-high SES group only. These data suggest that older adults with higher SES levels can use strategies to compensate for the adverse effects of aging in complex source memory tasks by recruiting additional neural resources apparently not required by the young.

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### 1. Introduction

Advanced age is often associated with adverse changes in memory functions (for reviews, see Craik and Bialystock, 2006; Fabiani et al., 2001; Friedman et al., in press; Kramer et al., 2006; Grady and Craik, 2000), but the aging process does not have an equal impact on all aspects of episodic memory. Whereas item memory (i.e. memory for the event itself) often appears relatively unaffected by advanced age, source memory (i.e. the conscious recollection of the context in which an event took place) is typically compromised (e.g. Fabiani and Friedman, 1997; Spencer and Raz, 1995; Trott et al., 1999). Notably, large individual differences exist among older adults in the extent to which their memory as well as other cognitive functions are preserved during aging. A number of

factors have been implicated as mediators of these individual differences, for example compensatory strategies (for review see Cabeza, 2002), intelligence and education (e.g. Shimamura et al., 1995; Lövdén et al., 2005; McDowell et al., 2004), cardiovascular fitness (e.g. Colcombe et al., 2004), reading ability (e.g. Manly et al., 2004) and reading activity (e.g. Wilson et al., 2003). Several studies have reported positive correlations between these variables, preserved performance on cognitive tasks, and a variety of underlying structural and functional brain measures, such that people with higher education may be better capable of counteracting the adverse effects of aging and/or coping with neuropathology (e.g. Springer et al., 2005). For example, the *cognitive reserve* hypothesis posits that certain individual characteristics will provide a buffer or reserve capacity protecting against the deleterious effects of aging on cognition and brain function (Stern, 2002; Stern et al., 1999). In the current study, we examined whether individual differences in

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SES (defined here as a combined score based on education and occupation (Watt, 1976) differentially affected the brain activity and performance of older adults in a task assessing recognition (item) and recency (source) memory. We hypothesized that older adults with higher SES would be more capable than older adults with low SES of using compensatory strategies to maintain relatively high levels of recency memory performance. As described below, the latter assesses the retrieval of temporal context, a memory function that is particularly compromised in older adults (Spencer and Raz, 1995). Further, based on fMRI and ERP evidence reviewed below, we hypothesized that these efforts would be accompanied by differential frontal brain activity in this group compared to older adults with low SES and young adults. To anticipate the findings, the results of the study support this hypothesis.

### 1.1. Source and item memory

An item's source can be defined as any of a number of contextual features that accompany the occurrence of an event, including perceptual (e.g., speaker's gender; Wilding and Rugg, 1996; picture's color; Cycowicz and Friedman, 2003) and temporal (e.g., sequential list in which the item occurred Trott et al., 1997) characteristics. Memory for contextual features, especially spatiotemporal aspects, appears to be particularly vulnerable to increasing age (Spencer and Raz, 1995), compared to simple recognition of the item as "old" (item memory). Because of this dissociation, it is useful to compare item and source memory within the same group. Continuous memory paradigms in which recognition and recency judgments are interleaved provide an elegant way of measuring the temporal source and item recognition aspects of memory in parallel, without confounding item and source memory performance with the effects of interference, practice and/or fatigue (Milner et al., 1991). In such paradigms, study and filler trials are intermixed with test trials. On test trials, subjects are instructed to make a forced choice about which of two items was presented more recently. When recognition memory is tested, only one of the two test probes has been presented before and is therefore the most recent, while the other is new. When recency memory is tested, both items have been presented earlier, albeit at different lags. Therefore, some information about the relative temporal occurrence of the two items has to be retrieved to support above-chance recency memory performance. A distinct advantage of this paradigm is that participants need not be aware of whether the test trial assesses recency or recognition memory, because the instruction to indicate the most recently presented item is identical in the two cases. Thus, any performance difference observed between recency and recognition cannot be attributed to differential task requirements.

A growing body of evidence links the ability to retrieve the contextual details of a memory trace to strategically based frontal lobe functions. For instance, Milner et al. (1991) found

that complex recency judgments were differentially affected by frontal and anterior temporal lobe lesions—frontal lesions impaired recency judgments, whereas neither frontal nor anterior temporal lesions affected recognition judgments. Similarly, patients with lesions in the dorsolateral frontal cortex have particular difficulty with memory for temporal order (Mangels, 1997). Since frontal lobe functions are known to deteriorate to some extent even in healthy aging (see Buckner, 2004; West, 1996 for reviews), Fabiani and Friedman (1997) used a variant of the paradigm described above to assess recency and recognition memory in groups of young and normally aging older adults. For pictorial stimuli, young and old adults performed equally well on recognition trials, but differed reliably on recency trials. Moreover, only the young had above-chance recency performance. As a converging source of information, recency memory performance was correlated with aspects of frontal lobe integrity (as indexed by WCST parameters), whereas recognition performance was not. Thus, the dissociation between recognition and recency memory in concert with the neuropsychological test results in a sample of healthy elderly provides support for the frontal lobe deficit hypothesis of cognitive aging and extends it to the temporal aspects of source memory performance (see also Trott et al., 1999; Wegesin et al., 2002). Neuroimaging studies based on positron emission tomography (PET) support these findings by indicating the activation of a network of prefrontal and posterior cortices during the retrieval of temporal order information (Cabeza et al., 1997, 2000). Hence, the reduced performance of the elderly in recency memory tasks could be related to reduced cortical thickness in frontal grey matter or to the disruption of white matter fiber tracts connecting frontal and posterior areas, both of which are frequently observed in healthy aging (e.g. Nordahl et al., 2006; Persson et al., 2006; Raz et al., 2005).

Although the exact role of the frontal cortex during recency memory remains to be established, the PFC appears to play a crucial role in the control of encoding and retrieval processes, particularly during source memory tasks (see Simons and Spiers, 2003 for a review). Consistent with the role of the left PFC for semantic retrieval processes (Thompson-Schill et al., 1997; Nessler et al., 2006), during source memory retrieval this region has been implicated in two important control operations. The first is the specification of relevant semantic retrieval cues based on the features of the potential sources (i.e. the use of semantic knowledge during episodic memory retrieval). The second is the subsequent evaluation of the products of the retrieval attempt based on their relevance for the source memory decision (Dobbins et al., 2002).

### 1.2. Individual differences in cognition and brain aging

Older adults on average show a decline of episodic memory function compared to younger adults, yet in some older individuals memory functions are largely preserved (e.g.

Shimamura et al., 1995). As a consequence, both performance and brain-related measures tend to show greater variability in older than younger adults (e.g. Lövdén et al., 2005; see Buckner, 2004 for a review). As noted, several mediator variables have been implicated in these individual differences, although the underlying mechanisms for preserved performance in old age are presently not completely understood. Since similar degrees of neuropathology do not necessarily lead to symptoms of comparable severity, it has been suggested that larger, relative to smaller, brains have greater reserve capacity to maintain efficient functioning despite neurological damage. This *brain reserve* hypothesis has been complemented more recently by a second, *cognitive reserve* hypothesis based on evidence that educational and occupational attainments can have similar protective effects, potentially by facilitating the use of alternate cognitive strategies (Stern et al., 1999; cf. Stern, 2002).

Hemodynamic studies of memory function suggest that performance might be preserved in older adults because they engage in different kinds of encoding and/or retrieval processing as indicated by activation of different neural circuits during episodic memory tasks relative to younger adults (for a review, see Reuter-Lorenz and Lustig, 2005). For instance, during recency memory retrieval predominantly right lateralized activation was observed in younger adults, whereas older adults showed a more bilateral activation pattern (Cabeza et al., 2000). Relative to younger participants, older adults have been reported to *underactivate* certain brain areas and/or *overactivate* others (see Buckner, 2004; Reuter-Lorenz and Lustig, 2005). Instances of overactivation have been suggested to underlie a compensatory mechanism that serves to reduce age-related episodic memory deficits (e.g. Cabeza et al., 2000; Grady and Craik, 2000). Both over- and under-activation tend to be most consistently observed in frontal regions (e.g. Reuter-Lorenz and Lustig, 2005), further supporting the idea that older subjects may engage in different strategic processes compared to the young, especially when memory tasks are challenging (see Cabeza, 2002).

The results of hemodynamic imaging studies have demonstrated that the left inferior prefrontal cortex (LIPFC) plays an important role in both the retrieval of semantic memories (e.g. Buckner et al., 2000a; Wagner et al., 2001) and the encoding of episodic memories (Buckner et al., 2000b). For example, the amount of activation is greater when semantic compared to orthographic features of verbal material must be retrieved (Kapur et al., 1994). Moreover, other investigations have shown that the amount of activation in this region during semantic retrieval tasks predicts better subsequent episodic memory performance compared to orthographic tasks (e.g. Grady et al., 1998; Tulving et al., 1994). Similarly, a left inferior frontal negativity has been implicated in the retrieval and selection of semantic attributes as well as episodic encoding in a recent ERP study (Nessler et al., 2006). A late (1200–1400 ms) left frontal negativity was dramatically reduced in older compared to young adults in

association with poorer subsequent episodic memory performance in the older adults. On these bases, it is likely that the hemodynamic underactivations (Gutchess et al., 2005; Logan et al., 2002) and the reduction in the left frontal negativity in older adults reflect a failure to activate LIPFC to a sufficient degree to enable older adults to deeply encode the items (e.g. through semantic elaborative activity), thereby resulting in poor subsequent episodic memory performance. Taken as a whole, these data suggest an important role for the left inferior prefrontal cortex in semantic retrieval and episodic encoding control processes.

By contrast with the underactivations reported during encoding, overactivations in similar left prefrontal areas have been found in hemodynamic studies of memory retrieval for all (e.g. Cabeza et al., 2000) or a subset of older participants with higher performance (e.g. Cabeza et al., 2002). Similarly, in two recent ERP studies of retrieval, older adults demonstrated a larger and temporally sustained left inferior frontal negativity that was not observed in the young (Nessler et al., in preparation; Swick et al., 2006). Although the distribution of ERP effects on the scalp does not allow firm conclusions about their neuronal origin, the fact that this latter negativity was absent for patients with left prefrontal lesions in (Swick et al., 2006) is consistent with a left-prefrontal cortex contribution to the negativity observed on the scalp.

Because the hemodynamic underactivations and reduced left frontal negativities observed during encoding presumably reflect reduced semantic elaboration (i.e., episodic encoding), it is conceivable that the retrieval-related left inferior frontal negativities reflect compensatory semantic elaborative processes that are engaged during retrieval (Nessler et al., in preparation) by older adults in an attempt to recover the initially poorly encoded information. However, the very limited data do not permit a firm conclusion at this time as to whether these retrieval-related frontal negativities are related to performance as predicted by a compensatory account. Further assessment of this possibility is one of the goals of this investigation.

Given the importance of efficient encoding- and retrieval-related strategies in the preservation of episodic memory performance, it is useful to examine brain activation patterns as a function of reserve factors which might be linked to strategy use. For example, recent fMRI data demonstrate that during an episodic memory task, older adults with higher levels of education engaged frontal brain structures more than medial temporal regions, but the reverse pattern was observed for young participants (Springer et al., 2005). Whereas the activation of frontal brain areas was correlated with poorer recognition accuracy in the young, it was associated with higher performance in the elderly. These data suggest that an alternative neuronal network characterized by increased engagement of prefrontal regions may underlie the enhanced recognition memory performance of highly-educated older adults (Springer et al., 2005).

To the authors' knowledge, no previous ERP study has compared groups of older participants as a function of reserve

factors such as SES or education. Thus, it is useful to examine how age-related changes in ERP activity may be linked to some of the potential factors mediating age-related preservation of memory function in order to establish under which conditions and for which tasks compensatory benefits are observed.

### 1.3. Aims and predictions of the current study

The goal of the present investigation was to determine whether SES would impact recency and recognition memory performance as well as the neural networks recruited for these tasks. We hypothesized that older adults who are characterized by higher levels of SES might be able to maintain the use of efficient retrieval strategies into old age. This, in turn, could support the preservation of source memory function. Because age-related decrements are most pronounced in source memory tasks that rely on the frontal lobes and their interconnections (e.g. [Dobbins et al., 2002](#)), a variation of the continuous recency/recognition paradigm described by [Fabiani and Friedman \(1997\)](#) was used. The current study is a follow-up of this earlier behavioral investigation with the addition of ERP recording. Due to the previous finding that the age-related dissociation between recency and recognition performance was most evident with pictorial stimuli, pictures of common objects were employed in the current investigation. Elderly participants were categorized into low- and high-SES groups based on a combined index of occupation and education and compared to a group of young adults. It was predicted that high levels of SES would have a positive influence on recency memory performance. Based upon recent fMRI and ERP data ([Springer et al., 2005](#); [Swick et al., 2006](#)), it was expected that the positive effect of SES on recency performance would be associated with frontally based ERP parameters, which would be of larger magnitude in the high-relative to low-SES groups. By contrast, it was expected that SES would not be related to performance and/or frontally oriented ERP modulations in the recognition task.

## 2. Methods

### 2.1. Participants

Fifteen young (age range = 18–26,  $M = 21$ ) and 15 older female participants (age range 65–82,  $M = 73$ ) were recruited by means of ads posted in local newspapers, and by notices posted within the Columbia Presbyterian Medical Center complex. The focus was placed on female participants because too few men volunteered for the study and/or met the inclusion criteria described below. All participants were paid \$10 h for their participation and signed informed consent. All were right-handed as assessed by self-report and by the Edinburgh Inventory ([Oldfield, 1971](#)), native English speakers, in good physical and mental health, and free from medications that are known to affect the central nervous system. Data from two participants (one old, one young) could not be included in the analyses due to excessive EEG artifacts. In order to assess whether SES would impact memory performance and ERP indices, the older adults were divided into two groups according to their SES ([Watt, 1976](#)). Traditionally, using this measure higher scores indicate lower SES. Here we transformed these values to make them more intuitive (i.e., higher scores correspond to a higher SES) by subtracting the original SES value from 100. This measure underestimates the index for young adults, who are continuing their education and, therefore, have not yet reached high levels of educational and occupational status (see [Table 1](#)).

### 2.2. Screening procedures

Participants were screened by means of a number of tests, and only participants who met pre-established criteria were admitted into the study. All participants were within normal limits on the modified Mini-mental status exam ([Mayeux et al., 1981](#)), and had at least average IQ (as assessed by an abbreviated form of the WAIS ([Satz and Mogel, 1962](#)), modified for the WAIS-R ([Adams et al., 1984](#))). In addition, older participants received a medical and neurological

Table 1

Mean ( $\pm$ S.D.) values of demographic and neuropsychological measures for young and old-high and old-low SES groups

	Young ( $N = 14$ )		Old-high SES ( $N = 7$ )		Old-low SES ( $N = 7$ )		Young vs. old-high SES	Old-high vs. old-low SES
	Mean	S.D.	Mean	S.D.	Mean	S.D.		
Age	21.36	2.50	72.86	3.72	73.86	7.82	***	ns
SES <sup>a</sup>	37.79	11.05	63.14	11.65	36.86	5.43	***	***
Years of education	15.00	1.74	17.71	4.19	14.07	1.37	ns	*
mMMS <sup>b</sup>	55.71	0.99	54.43	2.30	54.00	1.16	ns	ns
Boston naming	55.64	4.14	56.43	2.37	53.71	3.20	ns	ns
Vocabulary	61.57	4.96	65.71	2.98	62.14	3.85	ns	ns
Verbal IQ	118.21	8.90	123.29	10.34	113.71	7.63	ns	ns
Performance IQ	111.79	10.67	113.57	13.44	101.14	6.01	ns	ns
Full IQ	115.57	6.56	121.29	11.63	110.14	6.39	ns	*
Alternative categories	12.29	3.69	11.57	4.61	6.71	2.63	ns	ns

<sup>a</sup> Socio-economic status; modified from [Watt \(1976\)](#).

<sup>b</sup> Modified mini-mental state exam ([Mayeux et al., 1981](#)).

\*  $p < .05$ .

\*\*\*  $p < .0001$ .

assessment. This examination was conducted by a board-certified neurologist in order to assess prospective volunteers for the presence of neurodegenerative disorders, clinically detectable neurovascular disease, visual acuity, visual fields, disturbances in gait and the presence of tremors or rheumatologic disorders. All older participants were free of dementia, depression, and not limited in the activities of daily living as determined by a semi-structured interview, the Short-CARE (Gurland et al., 1984). Demographic and neuropsychological characteristics of the participants are presented in Table 1, along with the results of Tukey HSD post hoc tests to determine if between-group differences on the various measures were reliable. The old-high SES group did not differ from young adults on any of the screening instruments. The old-low and old-high-SES groups did not differ in age or mMMS scores. However, those with higher SES also had higher full scale IQs (Table 1).

### 2.3. Wisconsin Card Sorting Test (WCST)

The WCST was used as a putative measure of frontal lobe function, for which we expected individual differences, especially in the sample of older adults. The full version of the Wisconsin Card Sorting Test (2 decks of 64 cards) was administered to each subject (Heaton, 1981). Each of the cards is to be assigned to one of four groups, and participants have to deduce the correct sorting rule on the basis of “correct” versus “incorrect” feedback given by the experimenter. The sorting criterion is switched every 10 correct trials. Testing is discontinued when the criterion of 6 sorting categories is reached, after all 128 cards have been used, or if the subject cannot deduce the first sorting rule after 64 trials. Based on the results of a factor analysis of the WCST scores in relation to recency and recognition performance (Fabiani and Friedman,

1997), only the following WCST indices were used here: categories completed (ranging from 0 to 6), number of errors, perseverative errors, non-perseverative errors, perseverative responses and percent conceptual level responses (i.e. runs of three or more consecutive correct responses divided by the total number of trials times 100).

### 2.4. Stimuli and procedures

Pictures of common objects were used as stimuli (from Berman et al., 1989; Cycowicz et al., 1997; Snodgrass and Vanderwart, 1980). Four sequences (involving a rotation of the stimuli between recency and recognition trials) were used and were counterbalanced across participants. The stimuli were equated on name agreement across the four sequences. Instructions emphasized speed and accuracy equally, as well as the necessity to respond to all test trials. Stimuli were displayed for 2500 ms, with an ISI of 3000 ms.

Fig. 1 depicts a schematic sequence of study and test trials. Participants were presented with a continuous sequence of 505 trials. The first 111 trials were *information or study trials*. On each study trial, a stimulus was displayed in the center of the screen, and the subject was instructed to examine it for future memory testing. This initial study sequence was constructed so that test trials involving different lags could be randomly and uniformly distributed throughout the test sequence. This feature is crucial in order to avoid confounding differences in performance across lags and types of test trial (recency, recognition) due to fatigue and/or practice (which could also differentially affect younger and older adults). Starting with trial number 112, test trials were randomly intermixed with study trials (either 2 or 3 intervening study trials occurred between successive test trials). On *test trials*, two stimuli were displayed side by side (see Fig. 1), and

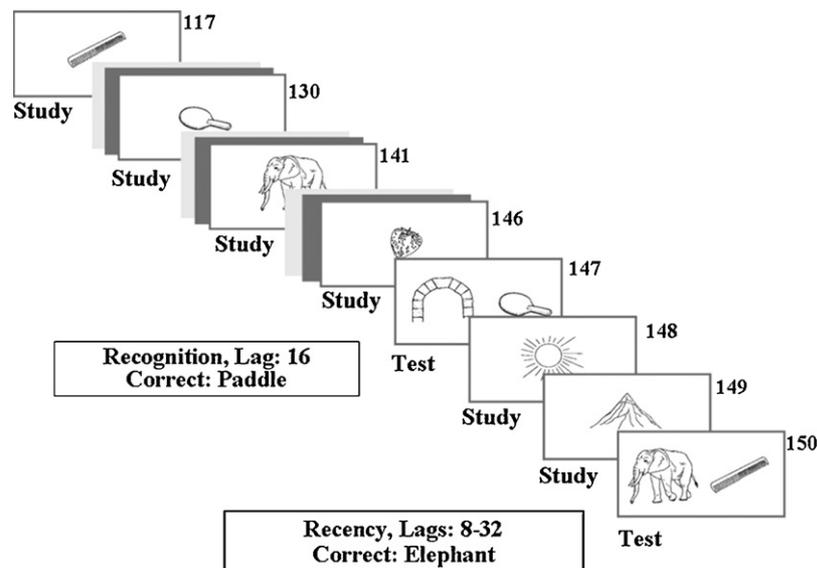


Fig. 1. Schematic description of the trial structure for the recency/recognition task. Trial 147 provides an example of a recognition trial (one old, one new item) and trial 150 illustrates a recency trial (two old items).

the subject was asked to indicate which of the two stimuli was presented most recently, by pressing the button corresponding to the side of the most recent picture. Some of these test trials contained two stimuli that had been previously presented at different lags (*recency trials*,  $N = 60$ ), whereas other test trials only had one old stimulus whereas the other was a new item (*recognition trials*,  $N = 60$ ). Items for recognition testing followed their initial presentation after short (4 or 8 intervening items), medium (16 or 32 intervening items) or long lags (64 or 128 intervening items). Unlike recognition performance, which decreases as lag increases, recency memory performance improves as the lag between first and second presentations increases. Hence, first and second presentations appeared with a ratio of 1:4 intervening items (8:32, 16:64, 32:128) or of 1:2 intervening items (4:8, 16:32, 64:128). For both recency and recognition, there were 10 trials tested at each lag. In order to increase the signal to noise ratios, ERP analyses were based on recency and recognition trials that had been collapsed across lags. For consistency, the same approach was used for the behavioral analysis. The side of stimulus presentation during test trials (and hence, the hand used for response) was counterbalanced across lags and type of test trial.

Preceding the experimental series, a short practice block consisting of 25 trials was administered. The practice trials were first administered with index cards to ensure that all participants understood the instructions, and to allow participants to ask clarifying questions. An identical practice sequence was then run on the computer to familiarize participants with the response box and the pace of the task. Pictures that had not been normed were used for the practice block and were not included in the experimental series.

### 2.5. EEG recording procedures

EEG was recorded from 30 placements (referred to as the nosetip) by means of an electrode cap (Electrocap International, Inc.) for the sites located on the scalp, and by means of disposable Ag/AgCl electrodes for sites located on the face and mastoids. In the figures depicted below, standard 10–20 placements were located at Fz, Cz, and Pz. The non-standard placements were as follows: Fp1' (16% of the distance on the midline from the back to the front of the cap in front of Fz and laterally on the left hemisphere 10% of the distance from ear to ear); F3' (33% of the distance on a line between Cz and F3 on the left hemisphere, closer to F3); C3' (60% of the distance on a line between Cz and C3 on the left hemisphere, closer to C3); P3' (65% of the distance on a line between Pz and P3 on the left hemisphere, closer to P3); Fp2', F4', C4' and P4' were placed homologous to these sites on the right hemisphere. Horizontal and vertical EOG were recorded bipolarly with electrodes placed, respectively, at the outer canthi of both eyes, and above and below the right eye. EOG and EEG were recorded with a bandpass of .01–30 Hz, and digitized at 200 Hz. Single trials were epoched off-line with 100-ms pre- and 2600-ms post-stimulus periods. Eye-

movement artifacts were corrected off-line (Gratton et al., 1983). In addition, single trials were visually inspected and trials containing muscular or other recording artifacts were marked and excluded from further analysis.

### 2.6. Data analyses

Behavioral analyses were conducted on accuracy scores and reaction times (RT) with mixed-design, repeated-measures ANOVAs. ERP averages were computed separately for correct recency and recognition test trials. Mean trial numbers for recency and recognition, respectively, were 33 and 44 for the young, 21 and 31 for the old-high SES, and 20 and 32 for the old-low SES group. ERP amplitudes were computed as averaged voltages within specified time windows with respect to the 100-ms pre-stimulus baseline. The amplitude measures were submitted to mixed-design, repeated-measures ANOVAs. Whenever appropriate, the Greenhouse–Geisser  $\epsilon$  correction for lack of sphericity was applied (Jennings and Wood, 1976). The degree of pairwise association between SES, WCST indices, recognition and recency accuracy and ERP amplitudes was evaluated by bivariate Pearson correlations. A one-tailed  $p$  value was used because all of our a priori hypotheses were directional. For example, as previously noted, we predicted that recency accuracy would be higher in those older adults with higher SES status. Because both measures that contribute to the SES index are systematically underestimated in the young, these correlations were computed only on the data of the older participants.

## 3. Results

### 3.1. Behavioral results

#### 3.1.1. WCST

Although the elderly in the high-SES group committed more errors, completed slightly fewer categories and produced slightly fewer conceptual level responses than the young (see Table 2), Tukey post hoc tests indicated that none of these differences was reliable (all  $ps > .60$ ). Old-low SES adults, however, committed a significantly larger number of errors and completed fewer categories with fewer conceptual level responses compared to both old-high SES (all  $ps < .01$ ) and young adults (all  $ps < .001$ ). The association between SES status and WCST performance was also evident in reliable correlations between SES and WCST number of errors ( $r(12) = -.50$ ), perseverative errors ( $r(12) = -.47$ ) and categories completed ( $r(12) = .47$ ), indicating that higher SES scores were associated with fewer errors and the correct completion of more categories, indicating better performance on the WCST (all  $ps < .05$ ).

#### 3.1.2. Recency/recognition judgments

The accuracy and RT data in the recency/recognition task can be found in Table 3. To determine whether accuracy

Table 2  
Mean ( $\pm$ S.D.) WCST indices for young and old with high and low SES

	Young		Old-high SES		Old-low SES		Young vs. old-high SES	Old-high vs. old-low SES
	Mean	S.D.	Mean	S.D.	Mean	S.D.		
Categories completed	6.00	0	5.86	0.38	3.71	2.29	ns	**
Number of errors	10.07	2.09	17.00	9.93	50.14	29.34	ns	**
Perseverative responses	5.93	1.98	11.00	8.45	33.29	26.42	ns	*
Perseverative errors	5.78	1.67	9.57	7.04	27.71	19.86	ns	**
Non-perseverative errors	4.29	1.59	7.43	3.64	22.43	19.94	ns	*

\*  $p < .05$ .

\*\*  $p < .01$ .

on recognition and recency trials differed between groups, an ANOVA with the factors of group (young, old-high SES, old-low SES) and Trial Type (recency, recognition) was conducted. Across recency and recognition trials, the main effect of group [ $F(2, 25) = 5.98, p < .01$ ] indicated reliable performance differences only between the young and old-low SES groups ( $p < .01$ ), as assessed by post hoc tests. Recency accuracy was lower than recognition accuracy for all three groups, as evident in a main effect of Trial Type [ $F(1, 25) = 125.47, p < .0001$ ]. Although the interaction between these variables was not reliable [ $F(2, 25) = 1.99, p = .16$ ], based on our a priori hypotheses, planned comparisons were performed to assess whether the old-high and old-low SES groups differed in recency and recognition memory accuracy. Post hoc tests confirmed that all three groups performed well on recognition trials with no reliable differences in accuracy (all  $ps > .57$ ). By contrast, on recency trials, older adults in the low-SES group performed reliably more poorly compared to both the old-high SES ( $p < .05$ ) and young ( $p < .0001$ ) adults. Importantly, old-high SES adults and young adults did not differ in recency accuracy ( $p = .53$ ).

We did not predict an interaction between SES group and Trial Type for RT. Consistent with this, an ANOVA with the factors of group (young, old-high SES, old-low SES) and Trial Type (recency, recognition) revealed no significant effects (all  $ps > .09$ ; see Table 3). To determine whether older adults as a whole showed reliable RT slowing relative to young adults, the two SES groups were collapsed and a  $t$ -test was performed. This analysis revealed that RTs were reliably longer for the elderly than the young (1384 versus 1177 ms,  $t(26) = 2.30, p < .05$ ).

The relations between accuracy on recency and recognition trials and SES were also examined by computing correlations between these variables on the data of the older adults. As predicted, accuracy on recency trials was highly correlated with SES ( $r(12) = .69, p < .01$ ), indicating that higher levels of SES were strongly associated with higher accuracy on recency trials. By contrast, the correlation between SES and recognition accuracy was not significant ( $r(12) = -.20, p = .24$ ). Recency accuracy was also related to WCST total number of errors ( $r(12) = -.48$ ) and number of perseverative errors ( $r(12) = -.48$ ), indicating that higher recency performance was associated with fewer errors on the WCST (both  $ps < .05$ ). This was not true for recognition accuracy (both  $ps > .15$ ). Critically, the correlation between recency accuracy and SES was still reliable when each of the performance indices from the WCST was partialled out (all  $rs(11) > .61$ , all  $ps < .05$ ), suggesting that the association between SES and recency accuracy was not mediated solely by the functions indexed by the WCST.

To summarize, old-low SES participants had lower performance than the old-high SES and young adult groups on recency trials, despite equivalently high performance on recognition trials. Importantly, the old-high SES group did not differ from the young in recency performance. The relation between SES and recency accuracy in the data of the older adults was confirmed by a significant correlation between these variables on recency, but not recognition trials. Moreover, reliable correlations between WCST indices and recency performance provide some limited support for the hypothesis that recency memory may be supported by contributions from the frontal lobes and their interconnections. However, the indices reflected by the WCST do not

Table 3  
Mean ( $\pm$ S.D.) recency/recognition accuracy and reaction times for young, old-high and old-low SES

	Young		Old-high SES		Old-low SES		Young vs. old-high SES	Old-high vs. old-low SES
	Mean	S.D.	Mean	S.D.	Mean	S.D.		
Percent correct (PC) recency	63.05	5.40	60.04	6.05	51.28	6.94	ns	*
PC recognition	83.79	6.71	80.07	7.62	80.91	10.23	ns	ns
RT recency (ms)	1180	199	1394	210	1360	394	ns	ns
RT recognition (ms)	1175	186	1423	152	1355	333	ns	ns

\*  $p < .05$ .

appear to be the sole mediator of the effects of SES on recency accuracy.

### 3.2. ERP results

The ERP waveforms for the three groups are illustrated in Fig. 2A–C. The ERPs are depicted on a time base of 1700 ms with 100-ms pre- and 1600-ms post-stimulus intervals. A long-duration negativity can be observed over frontal electrode sites in the ERPs of both groups of older adults. Importantly, starting around 500 ms and lasting until about 1500 ms, this negativity is larger for recency relative to recognition trials in the ERPs of the old-high SES group only. The difference in negative activity due to retrieving recency information appears to be larger over left-frontal electrode sites (see scalp map in Fig. 2C). For young adults, both recency and recognition trials elicit a prominent positivity, the P3b, peaking between 300 and 700 ms with a maximum over parietal

electrode sites. This P3b is less pronounced in both groups of older adults, consistent with previous findings (e.g., Fabiani and Friedman, 1995; Friedman et al., 1997; see also Fabiani et al., 1998). We did not predict an association between the P3b and Trial Type and none was found [ $F(1, 25) = 2.72, p > .11$ ]. Therefore, the following analyses focus only on frontal negative slow wave activity. Main effects of Hemisphere and/or Anterior/Posterior (see below) are not reported unless they interacted with group or Trial Type as, by themselves, they are not relevant to the hypotheses under study.

Because of a lack of visually observed differences in scalp distribution across the long time period when the negative slow wave was active, it was measured as an averaged voltage between 800 and 1500 ms. The averaged voltage measures were subjected to a group (young, old-high SES, old-low SES) by Trial Type (recognition, recency correct) by Hemisphere (left, right) by Anterior/Posterior (frontopolar, frontal, central, parietal) ANOVA. The latter two factors consisted of

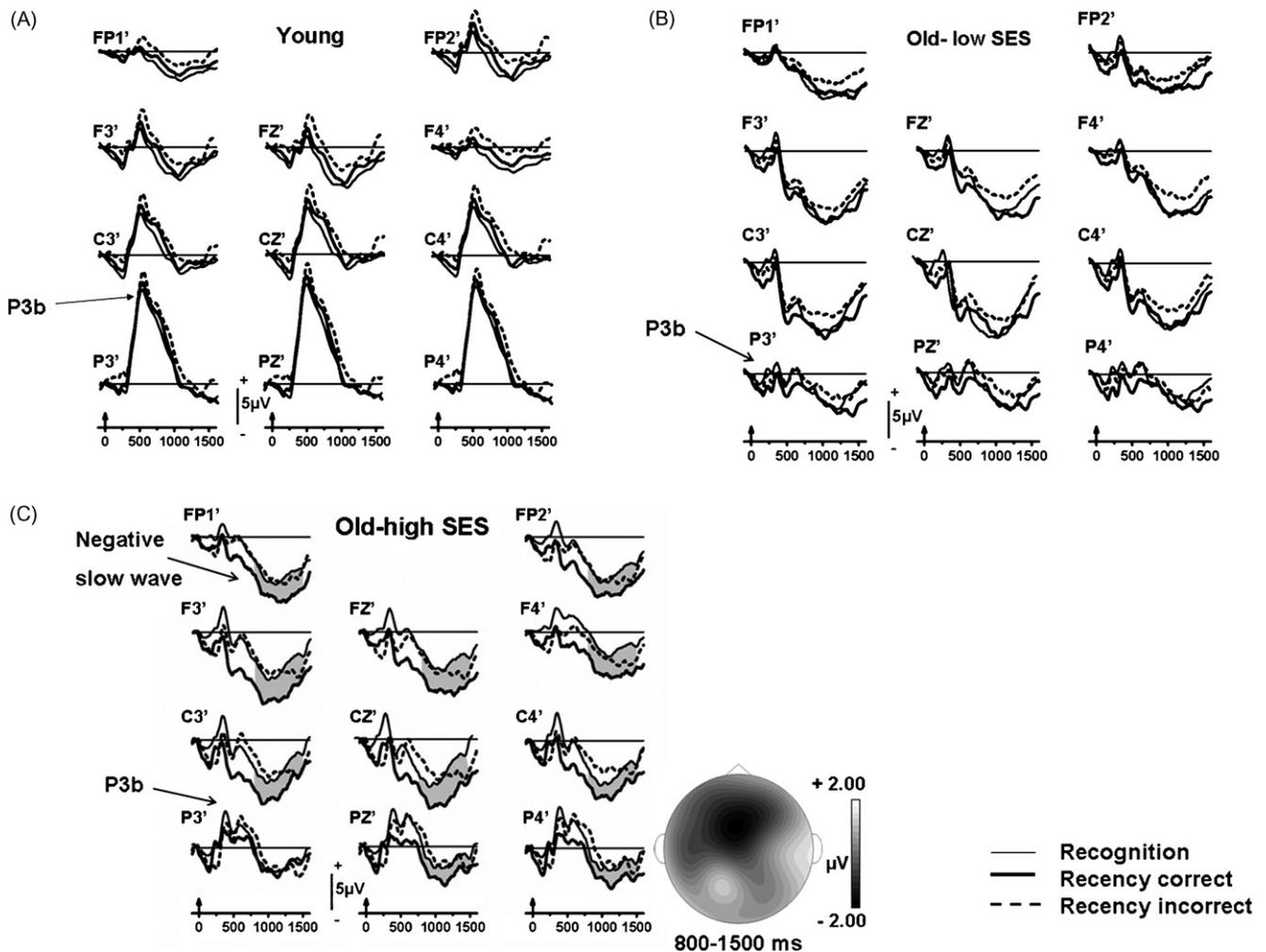


Fig. 2. Grand mean ERP data at selected frontal electrode sites for the young (A), old-low SES (B) and old-high SES (C) groups. Recency trials are depicted in thick solid lines, recognition trials in thin solid lines, and incorrect recency trials in dashed lines. The difference between correct recency and recognition trials was evaluated as an averaged voltage between 800 and 1500 ms (shaded region of the ERPs in (C)). The difference in negative slow wave activity had a left frontal topography ((C) averaged voltage map at right) and was not evident for incorrect recency trials. Arrows mark stimulus onset, with time lines indicated every 250 ms.

the electrode locations FP1', FP2', F3', F4', C3', C4', P3' and P4'. This analysis revealed a trend for an interaction between group and Trial Type [ $F(2, 25) = 2.96, p = .07$ ] with no reliable main effects of Trial Type or group. Because of our a priori prediction that only old-high SES participants would show frontally-based ERP modulations that would be associated with enhanced recency performance, planned comparisons in the form of Trial Type by Hemisphere by Anterior/Posterior ANOVAs were performed for each group separately. No reliable main or interaction effects of Trial Type were found for the young or old-low SES groups (all  $F_s < 1$ ). However, for the old-high SES group, a main effect of Trial Type [ $F(1, 6) = 10.33, p < .05$ ] was obtained, which did not interact with any of the remaining factors ( $F_s < 1.35$ ). In order to determine where the difference in negativity was largest, simple effects ANOVAs were performed at each of the Anterior/Posterior regions. Consistent with the frontal topography of this activity, these revealed that the effect of Trial Type was reliable at frontopolar [ $F(1, 6) = 11.67, p < .05$ ], frontal [ $F(1, 6) = 9.78, p < .05$ ] and central [ $F(1, 6) = 7.52, p < .05$ ] electrode sites, but not at parietal sites ( $F < 1$ ).

In a next step, we evaluated whether the observed slow wave merely reflected the increased complexity of recency trials or was associated with *successful* recency memory. If the latter were true, it could be concluded that the reliable differential activity seen in the old-high SES group had functional relevance consistent with a compensation account. To address this question, we examined whether the slow wave was also present for incorrect recency trials, for which equivalent complexity relative to correct trials could be assumed. The corresponding waveforms for incorrect recency trials are depicted in Fig. 2A–C for all three groups. However, this analysis was restricted to the old-high SES group, because no reliable left frontal negative difference was found for the old-low SES group or the younger adults. In the old-high SES group, the negative slow wave to incorrect recency trials (mean trial number = 15) was compared to that associated with correct recognition trials in a Trial Type (recognition, recency incorrect) by Hemisphere (left, right) by Anterior/Posterior (frontopolar, frontal, central, parietal) ANOVA. No reliable differences were found (all  $F_s < 1$ ), supporting the notion that the negative difference observed selectively in the old-high SES group was related to successful recency memory performance.

The degree of association between the frontal negative slow wave and performance accuracy was further examined by computing the correlation between recency accuracy and the magnitude of the recency/recognition difference at frontopolar, frontal and central electrode sites. The correlations were computed only on the data of the old-high SES group because the other groups did not show a reliable difference in negative activity between recency and recognition trials. Whereas no reliable correlations were observed for recognition accuracy (all  $r_s < .10$ ), recency accuracy was closely associated with the magnitude of the recency/recognition dif-

ference at FP1 ( $r(5) = .70, p < .05$ ), indicating that higher recency performance was associated with a larger negative difference between recency and recognition trials. This association was somewhat smaller at the remaining electrode sites (all  $r_s > .57$  and  $< .64$ ), where it was evident as a trend (all  $p_s > .05$  and  $< .09$ ). No reliable correlations were found between recency accuracy and the absolute magnitude of the negativity for recency trials (all  $p_s > .30$ ), consistent with the hypothesis that the difference between the conditions is functionally relevant to performance accuracy on recency trials.

To summarize, the analyses of the ERP data supported the observation that a frontal negative slow wave associated with correct recency relative to recognition trials was present only in the old-high SES group. It was not associated with recency per se, consistent with its relation to successful performance as predicted by a compensation account.

#### 4. Discussion

In the present study, the potential role of higher SES in maintaining relatively high performance levels in a challenging recency memory task was explored by classifying a group of older participants into high and low SES subgroups. Old-high and old-low SES groups did not differ from each other or from younger participants in accuracy on item recognition trials. However, only the old-high SES group performed equivalently to the young during recency memory trials. This relation was also evident in high correlations between recency memory performance and SES, which were not reliable for recognition accuracy. Similarly, the old-high SES, but not the old-low SES group, scored as well as the young on selected WCST indices. Further, higher recency accuracy was associated with higher WCST performance and greater magnitude negative slow wave activity. These associations are consistent with the idea that recency memory relies to a larger extent on frontal lobe function than recognition memory. Although the use of the WCST as a pure measure of frontal function has not gone unchallenged (Mountain, 1993), it does provide an independent, though limited, piece of evidence that the difference between the old-high and old-low SES groups may lie in the ability to recruit prefrontal resources to support recency memory performance. On the other hand, the fact that the correlation between SES and recency performance was still reliable and of similar magnitude after controlling for performance on the WCST, suggests that the processes reflected by the WCST may not have been the primary contributors to the association between SES and recency memory. Indeed, a negative slow wave maximal over frontal scalp locations was observed for correct recency relative to recognition trials only in the old-high SES group. Both its timing (with onset around 500 ms, well before the mean RT of  $\sim 1400$  ms), and the lack of difference between incorrect recency and correct recognition trials are consistent with the notion that the additional negative activity could have supported successful recency performance in the old-high SES

group. Moreover, the results of the present investigation are in line with previous hemodynamic (Cabeza et al., 2000) and behavioral (Fabiani and Friedman, 1997) studies demonstrating age-related differences in recency memory in the absence of reliable age differences in item recognition performance. Concordant with more recent hemodynamic neuroimaging studies, these data provide evidence for additional frontal activity in a subset of elderly participants in association with higher memory accuracy (cf. Cabeza et al., 2002) and higher levels of educational attainment (cf. Springer et al., 2005).

To the authors' knowledge, this is the first ERP study to report an association between left-frontal slow wave activity and higher memory accuracy in a subgroup of healthy older participants. Given the increased variability of memory functions in old age (Buckner, 2004; Lövdén et al., 2005), the fact that others have not reported similar differences between subgroups of older participants is somewhat surprising. However, a few factors could potentially account for this apparent discrepancy. In neuroimaging investigations of aging, the samples of elderly under examination typically represent very healthy and cognitively intact individuals due to self-selection and relatively rigorous exclusionary criteria. This homogeneity could mask the presence of compensatory processes, which would most likely be observed in comparisons involving less well-educated and cognitively intact individuals of the same age. These latter individuals typically do not volunteer for (or are excluded from) laboratory studies of cognitive aging, and only very few ERP investigations of the cognitive aging of memory have compared subgroups of older participants (for an example see Duarte et al., 2006). Moreover, in the current study compensatory retrieval strategies may have been employed because strategies for efficient encoding of the information were not provided through experimental instruction, and the former may have been available only to the old-high SES group (see Logan et al., 2002 and Section 4.2). Finally, the relatively low accuracy rate in the young group suggests that the continuous recency memory paradigm used here was more challenging than most other paradigms, including those that assess other forms of source memory.

#### 4.1. Evidence for the negative slow wave reflecting compensatory activity

Despite recent evidence for successful compensation in some (e.g., better-educated older adults; Springer et al., 2005), there is still considerable debate about whether increased neuronal recruitment is always a marker of compensatory activities or can sometimes index decline or early stages of neuropathology (for reviews, see Cabeza, 2002; Friedman, 2003; Reuter-Lorenz and Lustig, 2005; see also Fabiani et al., 2006). According to the *dedifferentiation* view, additional activation in the elderly is a consequence of difficulty in recruiting specialized neural mechanisms that are normally recruited by the young (Colcombe et al., 2005; see Cabeza, 2002 for a review), which could be due, in part, to

an age-related deterioration of neurotransmitter systems (cf. Li et al., 1999).

In contrast, successful compensation is associated with a dissociation of performance levels and brain activation patterns between groups, since high performance is supported by levels of brain activity in the young that may not be sufficient to support the same performance in the old. This is presumably a consequence of age-related physiological changes that are not severe enough to completely disrupt performance (see Buckner, 2004 for a review).

The current ERP data appear to support the compensation view. Four main arguments point to the functional relevance of the negative slow wave for the enhanced recency performance in the old-high SES group. First, if demographic differences, such as age or intellectual level were responsible for the ERP and behavioral differences between old-low and old-high SES groups, such differences would be expected on recognition as well as recency trials. By contrast, old-high versus old-low SES group differences in behavioral and ERP indices were only evident on the more challenging recency memory trials. Second, the negative frontal slow wave is not likely to be a reflection of increased difficulty *per se*, because it was not present for incorrect recency trials, which are likely of equal or greater difficulty. Third, the magnitude of the difference in negative slow wave activity was correlated with recency, but not recognition accuracy. Finally, Cabeza et al. (1997) provided related evidence in a PET study with young participants by demonstrating that blood flow distinguished between item and recency memory (i.e. predominantly medial temporal regions for item memory versus dorsolateral prefrontal and right posterior parietal regions for recency memory), but was independent of difficulty level in both tasks (Cabeza et al., 1997). Taken together, these data support the hypothesis of the functional relevance of the frontal negative slow wave in the maintenance of above-chance recency performance in the old-high SES group.

#### 4.2. The role of the frontal lobes in strategy use

As noted earlier, the difficulties with recency memory at older ages could be closely related to the adverse effects of aging on the frontal lobes, with grey matter loss accentuated in frontal areas of the brain. In addition, white matter degradation functionally disrupts frontal pathways (Buckner, 2004; Nordahl et al., 2006; Raz et al., 2005). Because the maintenance of recency performance appears to be mediated, at least in part, by the recruitment of frontal cortical mechanisms (Cabeza et al., 1997, 2002; Mangels, 1997; Milner et al., 1991; Springer et al., 2005), the engagement of appropriate strategies during this task appears to be critical.

A major contribution of the PFC to source memory retrieval is control processes, such as the specification of relevant (semantic) retrieval cues (Dobbins et al., 2002). During more typical source memory paradigms, distinct physical item features identify the two sources (e.g. color; Cycowicz and Friedman, 2003, or speaker's voice; Wilding and Rugg,

1996). However, in recency memory paradigms such distinct physical features are not necessarily available as the temporal order of presentation is the critical piece of information that needs to be retrieved. Hence, for these temporal episodes, it can be arguably difficult to specify a relevant retrieval cue. Nonetheless, the left frontal focus of the negative slow wave observed here is consistent with semantic retrieval control processes, which have been associated with the left prefrontal cortex (Dobbins et al., 2002), as described earlier and below.

One example of a successful retrieval strategy for the recency task might have been the retrieval of as many contextual details as possible. It is conceivable that the old-high SES group managed to encode more semantic attributes during study trials than their old-low SES peers. This, in turn, could have enabled them to retrieve those previously activated semantic features and compare which of them had been activated more recently by assessing the relative strength of activation. This explanation is consistent with the finding that the retrieval and selection of semantic features has been associated with left inferior prefrontal activity in hemodynamic (e.g. Thompson-Schill et al., 1997) as well as ERP (Nessler et al., 2006) investigations. Whereas individuals differ in the types of strategies they will spontaneously use when faced with challenging tasks, it is currently unclear whether the group differences we observed could have been reduced by providing instructions as to how to encode the items, for example, by using a deep, semantic encoding task (see e.g. Logan et al., 2002). If this were the case, episodic encoding and retrieval might be amenable to training which would aid in maintaining performance on those challenging activities that are essential for successfully navigating everyday life.

#### 4.3. Evidence for reserve mechanisms or compensation?

It is worth noting that both frameworks – the brain or cognitive reserve hypothesis and a compensatory account – explicitly mention alternate strategies as a possible underlying mechanism. As discussed earlier, the reserve hypothesis emphasizes performance maintenance (despite the decline expected on the basis of chronological age) as a result of challenging daily activities (as reflected for example by educational attainment as a proxy for cognitive reserve) or physiological characteristics (as reflected, for instance, by larger initial brain size). By contrast, the concept of compensation implies a discrepancy between task requirements and processing resources in specialized brain areas that have been adversely affected by advancing age (i.e. age-related neuropathology), which eventually results in the recruitment of additional brain regions.

One valid objection to the reserve hypothesis is the possibility that those older adults with superior memory performance relative to their peers might be those who always had superior memory performance from childhood, which they maintain into old age. A recent MRI study by Staff et al. (2004) tested this hypothesis empirically. In order to dissociate the protective effects of three proxies for reserve (total

brain volume, education and occupational attainment) from pre-existing differences in the level of cognitive ability, a large sample of elderly volunteers whose cognitive abilities had been evaluated previously at age 11 was re-examined at age 79. Along with a longitudinal re-assessment of memory functions, total brain volume and signs of neuropathology (i.e. white matter hyperintensities) were measured. Even when both childhood cognitive functioning and signs of age-related neuropathology were controlled for, both education and occupational attainment each still contributed about 5% of the variance to memory function in old age. On the contrary, there was no evidence for a protective role of larger total intracranial brain volume as proposed by brain reserve capacity models. Hence, this study provides empirical evidence for the protective effect of education and occupation above and beyond differences in individual memory abilities that had been present in childhood (Staff et al., 2004).

It is impossible to address the extent to which pre-existing performance differences maintained from a younger age contributed to the performance differences in old age in the current study. However, this explanation is unlikely, since all three groups performed equally well on item recognition trials, which would not be expected based on the assumption of different pre-existing memory abilities in the two older age groups.

#### 4.4. Which aspects of SES are critical?

A variety of other factors aside from educational and occupational attainment are closely associated with SES, such as access to health care and healthy nutrition throughout one's lifetime. In particular, poor childhood SES predicts poor adult health as well as lower education and adult income (Luo and Waite, 2005). In more extreme cases, it can be associated with the experience of chronic stress and, as a result, with elevated cortisol levels (Lupien et al., 2005). Chronically elevated levels of glucocorticoids in turn lead to memory impairments and reductions in hippocampal volumes (Lupien et al., 2005). In animal studies, consequences of long-term exposure to high levels of stress hormones include low spatial memory (see e.g. Montaron et al., 2006) as well as a decline in hippocampal neurogenesis (Yevgenia and Elizabeth, 2003). This line of argumentation suggests that the association between adult SES and impaired cognition in advanced age might, at least in part, rest on higher stress levels throughout life. These would eventually take their toll in old age when a decline in the number of newly formed hippocampal neurons might have a noticeable negative impact on cognition (Yevgenia and Elizabeth, 2003). Another aspect in this line of reasoning is noteworthy, namely that several risk factors often co-occur. For example, in a sample of elderly nuns, those with small head circumference in combination with lower education were four times as likely to be demented as the rest of the sample (Mortimer et al., 2003). Although the differences in SES in the present sample were moderate, in the challenging recency task differences between old-high and old-low

SES participants became apparent. Population-based studies could be expected to reveal effects of larger magnitude which might also be evident in less challenging tasks.

One factor that has been implicated repeatedly in mitigating cognitive decline in advanced age is education (e.g. Mortimer et al., 2003; Shimamura et al., 1995; Springer et al., 2005). Education appears to mediate performance preservation via protective mechanisms that serve to promote more cognitively challenging daily activities or the use of alternative strategies (e.g. Springer et al., 2005). Furthermore, it is conceivable that different aspects of cognitive performance are sensitive to other protective factors. A recent study using latent growth models provides evidence that social activities can alleviate age-related decline in perceptual speed (Lövdén et al., 2005). A variety of lifestyle choices such as maintaining physical fitness (e.g. Colcombe et al., 2004; Gordon et al., submitted) and engaging in mentally challenging activities (e.g. Wilson et al., 2000, but see Salthouse, 2006) could prove predictive of preserved performance in advanced age.

#### 4.5. Conclusions

Although the present investigation requires replication with larger sample sizes, extension to other aspects of episodic memory, and the recruitment of groups at the two extremes of the SES dimension, these results nevertheless illustrate that higher SES levels are associated with age-related memory preservation in a challenging recency task. Differences in frontal functioning between the two groups of older adults are consistent with the notion that alternate strategies underlie the superior performance in the old-high SES group. The current data provide evidence that demographic factors, such as educational level and occupational status, can influence how the brain copes with the adverse effects of aging.

#### Disclosure statements

1. There are no actual or potential conflicts of interest that could inappropriately influence the work of the authors. None of the author's institutions has any contracts relating to this research through which it or any other organization may stand to gain financially now or in the future.
2. This research was supported by the New York State Department of Mental Hygiene.
3. The data contained in the manuscript being submitted have not been previously published, have not been submitted elsewhere and will not be submitted elsewhere while under consideration at *Neurobiology of Aging*.
4. This research has been conducted in accordance with APA ethical standards for the treatment of human subjects. All subjects provided informed consent.
5. All authors have reviewed the contents of the manuscript being submitted, approve of its contents and validate the accuracy of the data.

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#### References

- Adams, R.L., Smigielski, J., Jenkins, R.L., 1984. Development of the Satz-Mogel short form of the WAIS-R. *J. Consult. Clin. Psychol.* 52, 908.
- Berman, S., Friedman, D., Hamberger, M., Snodgrass, J.G., 1989. Developmental picture norms: relationships between name agreement, familiarity and visual complexity for child and adult ratings of two sets of line drawings. *Behav. Res. Meth. Instr. Comp.* 21, 371–382.
- Buckner, R.L., Koutstaal, W., Schacter, D.L., Rosen, B.R., 2000a. Functional MRI evidence for a role of frontal and inferior temporal cortex in amodal components of priming. *Brain* 123, 620–640.
- Buckner, R.L., Logan, J., Donaldson, D.I., Wheeler, M.E., 2000b. Cognitive neuroscience of episodic memory encoding. *Acta Psychol. (Amst.)* 105, 127–139.
- Buckner, R.L., 2004. Memory and executive function in aging and AD: multiple factors that cause decline and reserve factors that compensate. *Neuron* 44, 195–208.
- Cabeza, R., Mangels, J., Nyberg, L., Habib, R., Houle, S., McIntosh, A.R., Tulving, E., 1997. Brain regions differentially involved in remembering what and when: a PET study. *Neuron* 19, 863–870.
- Cabeza, R., Anderson, N.D., Houle, S., Mangels, J.A., Nyberg, L., 2000. Age-related differences in neural activity during item and temporal-order memory retrieval: a positron emission tomography study. *J. Cogn. Neurosci.* 12, 197–206.
- Cabeza, R., 2002. Hemispheric asymmetry reduction in older adults: the HAROLD model. *Psychol. Aging* 17, 85–100.
- Cabeza, R., Anderson, N.D., Locantore, J.K., McIntosh, A.R., 2002. Aging gracefully: compensatory brain activity in high-performing older adults. *Neuroimage* 17, 1394–1402.
- Colcombe, S.J., Kramer, A.F., Erickson, K.I., Scalf, P., McAuley, E., Cohen, N.J., Webb, A., Jerome, G.J., Marquez, D.X., Elavsky, S., 2004. Cardiovascular fitness, cortical plasticity, and aging. *Proc. Natl. Acad. Sci. U.S.A.* 101, 3316–3321.
- Colcombe, S.J., Kramer, A.F., Erickson, K.I., Scalf, P., 2005. The implications of cortical recruitment and brain morphology for individual differences in inhibitory function in aging humans. *Psychol. Aging* 20, 363–375.
- Craik, F.I., Bialystock, E., 2006. Cognition through the lifespan: mechanisms of change. *Trends Cogn. Sci.* 10, 131–138.
- Cycowicz, Y.M., Friedman, D., Rothstein, M., Snodgrass, J.G., 1997. Picture naming by young children: norms for name agreement, familiarity, and visual complexity. *J. Exp. Child Psychol.* 65, 171–237.
- Cycowicz, Y.M., Friedman, D., 2003. Source memory for the color of pictures: event-related brain potentials (ERPs) reveal sensory-specific retrieval-related activity. *Psychophysiology* 40, 455–464.
- Dobbins, I.G., Foley, H., Schacter, D.L., Wagner, A.D., 2002. Executive control during episodic retrieval: multiple prefrontal processes subserve source memory. *Neuron* 35, 989–996.
- Duarte, A., Ranganath, C., Trujillo, C., Knight, R.T., 2006. Intact recollection memory in high-performing older adults: ERP and behavioral evidence. *J. Cogn. Neurosci.* 18, 33–47.
- Fabiani, M., Friedman, D., 1995. Changes in brain activity patterns in aging: the novelty oddball. *Psychophysiology* 32, 579–594.

- Fabiani, M., Friedman, D., 1997. Dissociations between memory for temporal order and recognition memory in aging. *Neuropsychologia* 35, 129–141.
- Fabiani, M., Friedman, D., Cheng, J.C., 1998. Individual differences in P3 scalp distribution in older adults, and their relationship to frontal lobe function. *Psychophysiology* 35, 698–708.
- Fabiani, M., Wee, E., 2001. Age-related changes in working memory function: a review. In: Nelson, C., Luciana, M. (Eds.), *Handbook of Developmental Cognitive Neuroscience*, vol. 473–488. MIT Press.
- Fabiani, M., Low, K.A., Wee, E., Sable, J.J., Gratton, G., 2006. Reduced suppression or labile memory? Mechanisms of inefficient filtering of irrelevant information in older adults. *J. Cogn. Neurosci.* 18, 637–650.
- Friedman, D., Kazmerski, V.A., Fabiani, M., 1997. An overview of age-related changes in the scalp distribution of P3b. *Electroencephalogr. Clin. Neurophysiol.* 104, 498–513.
- Friedman, D., 2003. Cognition and aging: a highly selective overview of event-related potential (ERP) data. *J. Clin. Exp. Neuropsychol.* 25, 702–720.
- Friedman, D., Nessler, D., Johnson, R., Jr., in press. Memory encoding and retrieval in the aging brain. *Clin. EEG Neurosci.*
- Gordon, B., Rykhlevskaia, E., Brumback, C.R., Lee, Y., Elavsky, S., Konopack, J.F., McAuley, E., Kramer, A.F., Colcombe, S., Gratton, G., Fabiani, M., submitted for publication. Anatomical correlates of aging, cardiopulmonary fitness level, and education.
- Grady, C.L., McIntosh, A.R., Rajah, M.N., Craik, F.I., 1998. Neural correlates of the episodic encoding of pictures and words. *Proc. Natl. Acad. Sci. U.S.A.* 95, 2703–2708.
- Grady, C.L., Craik, F.I., 2000. Changes in memory processing with age. *Curr. Opin. Neurobiol.* 10, 224–231.
- Gratton, G., Coles, M.G.H., Donchin, E., 1983. A new method for off-line removal of ocular artifact. *Electroencephalogr. Clin. Neurophysiol.* 55, 468–484.
- Gurland, B., Golden, R.R., Teresi, J.A., Challop, J., 1984. The SHORT-CARE: an efficient instrument for the assessment of depression, dementia and disability. *J. Gerontol.* 39, 166–169.
- Gutchess, A.H., Welsh, R.C., Hedden, T., Bangert, A., Minear, M., Liu, L.L., Park, D.C., 2005. Aging and the neural correlates of successful picture encoding: frontal activations compensate for decreased medial-temporal activity. *J. Cogn. Neurosci.* 17, 84–96.
- Heaton, R.K., 1981. *Wisconsin Card Sorting Test Manual*. Psychological Assessment Resources, Inc.
- Jennings, J.R., Wood, C.C., 1976. Letter: the epsilon-adjustment procedure for repeated-measures analyses of variance. *Psychophysiology* 13, 277–278.
- Kapur, S., Craik, F.I., Tulving, E., Wilson, A.A., Houle, S., Brown, G.M., 1994. Neuroanatomical correlates of encoding in episodic memory: levels of processing effect. *Proc. Natl. Acad. Sci. U.S.A.* 91, 2008–2011.
- Kramer, A.F., Fabiani, M., Colcombe, S., 2006. Contributions of cognitive neuroscience to the understanding of behavior and aging. In: Birren, J., Schaie, K. (Eds.), *Handbook of the Psychology of Aging*, vol. 57–83, 6th ed. Academic Press.
- Li, S.-C., Lindenberger, U., 1999. Cross-level unification: a computational exploration of the link between deterioration of neurotransmitter systems and dedifferentiation of cognitive abilities in old age. In: Nilsson, L.-G., Markowitsch, H.J. (Eds.), *Cognitive Neuroscience of Memory*, vol. 103–146. Hogrefe.
- Logan, J.M., Sanders, A.L., Snyder, A.Z., Morris, J.C., Buckner, R.L., 2002. Under-recruitment and nonselective recruitment: dissociable neural mechanisms associated with aging. *Neuron* 33, 827–840.
- Lövdén, M., Ghisletta, P., Lindenberger, U., 2005. Social participation attenuates decline in perceptual speed in old and very old age. *Psychol. Aging* 20, 423–434.
- Luo, Y., Waite, L.J., 2005. The impact of childhood and adult SES on physical, mental, and cognitive well-being in later life. *J. Gerontol. B: Psychol. Sci. Soc. Sci.* 60, S93–S101.
- Lupien, S.J., Fiocco, A., Wan, N., Maheu, F., Lord, C., Schramek, T., Tu, M.T., 2005. Stress hormones and human memory function across the lifespan. *Psychoneuroendocrinology* 30, 225–242.
- Mangels, J.A., 1997. Strategic processing and memory for temporal order in patients with frontal lobe lesions. *Neuropsychology* 11, 207–221.
- Manly, J., Byrd, D., Touradji, P., Sanchez, D., Stern, Y., 2004. Literacy and cognitive change among ethnically diverse elders. *Int. J. Psychol.* 39, 47–60.
- Mayeux, R., Stern, Y., Rosen, J., Leventhal, J., 1981. Depression, intellectual impairment, and Parkinson disease. *Neurology* 31, 645–650.
- McDowell, I., Xi, G., Lindsay, J., Tuokko, H., 2004. Canadian study of health and aging: study description and patterns of early cognitive decline. *Aging Neuropsychol. Cogn.* 11, 149–168.
- Milner, B., Corsi, P., Leonard, G., 1991. Frontal-lobe contribution to recency judgements. *Neuropsychologia* 29, 601–618.
- Montaron, M.F., Drapeau, E., Dupret, D., Kitchener, P., Arousseau, C., Le Moal, M., Piazza, P.V., Abrous, D.N., 2006. Lifelong corticosterone level determines age-related decline in neurogenesis and memory. *Neurobiol. Aging* 27, 645–654.
- Mortimer, J.A., Snowdon, D.A., Markesbery, W.R., 2003. Head circumference, education and risk of dementia: findings from the Nun Study. *J. Clin. Exp. Neuropsychol.* 25, 671–679.
- Mountain, Snow, 1993. Wisconsin Card Sorting Test as a measure of frontal pathology: a review. *Clin. Neuropsychol.* 7, 108–118.
- Nessler, D., Johnson Jr., R., Bersick, M., Friedman, D., 2006. On why the elderly have normal semantic retrieval but deficient episodic encoding: a study of left inferior frontal ERP activity. *Neuroimage* 30, 299–312.
- Nessler, D., Johnson, R., Jr., Bersick, M., Friedman, D., in preparation. Encoding manipulations equalize recognition performance in young and old despite persistent differences in retrieval processing.
- Nordahl, C.W., Ranganath, C., Yonelinas, A.P., DeCarli, C., Fletcher, E., Jagust, W.J., 2006. White Matter Changes Compromise Prefrontal Cortex Function in Healthy Elderly Individuals. *J. Cogn. Neurosci.* 18, 418–429.
- Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia* 9, 97–113.
- Persson, J., Nyberg, L., Lind, J., Larsson, A., Nilsson, L.G., Ingvar, M., Buckner, R.L., 2006. Structure–function correlates of cognitive decline in aging. *Cereb. Cortex* 16, 907–915.
- Raz, N., Lindenberger, U., Rodrigue, K.M., Kennedy, K.M., Head, D., Williamson, A., Dahle, C., Gerstorf, D., Acker, J.D., 2005. Regional brain changes in aging healthy adults: general trends, individual differences and modifiers. *Cereb. Cortex*.
- Reuter-Lorenz, P.A., Lustig, C., 2005. Brain aging: reorganizing discoveries about the aging mind. *Curr. Opin. Neurobiol.* 15, 245–251.
- Salthouse, T.A., 2006. Mental exercise and mental aging. *Perspect. Psychol. Sci.* 1, 68–87.
- Satz, P., Mogel, S., 1962. An abbreviation of the WAIS for clinical use. *J. Clin. Psychol.* 18, 77–79.
- Shimamura, A.P., Berry, J.M., Mangels, J.A., Rusting, C.L., Jurica, P.J., 1995. Memory and cognitive – abilities in university professors – evidence for successful aging. *Psychol. Sci.* 6, 271–277.
- Simons, J.S., Spiers, H.J., 2003. Prefrontal and medial temporal lobe interactions in long-term memory. *Nat. Rev. Neurosci.* 4, 637–648.
- Snodgrass, J.G., Vanderwart, M., 1980. A standardized set of 260 pictures: norms for name agreement, image agreement, familiarity, and visual complexity. *J. Exp. Psychol. [Hum. Learn]* 6, 174–215.
- Spencer, W.D., Raz, N., 1995. Differential effects of aging on memory for content and context: a meta-analysis. *Psychol. Aging* 10, 527–539.
- Springer, M.V., McIntosh, A.R., Winocur, G., Grady, C.L., 2005. The relation between brain activity during memory tasks and years of education in young and older adults. *Neuropsychology* 19, 181–192.
- Staff, R.T., Murray, A.D., Deary, I.J., Whalley, L.J., 2004. What provides cerebral reserve? *Brain* 127, 1191–1199.
- Stern, Y., Albert, S., Tang, M.X., Tsai, W.Y., 1999. Rate of memory decline in AD is related to education and occupation: cognitive reserve? *Neurology* 53, 1942–1947.

- Stern, Y., 2002. What is cognitive reserve? Theory and research application of the reserve concept. *J. Int. Neuropsychol. Soc.* 8, 448–460.
- Swick, D., Senkfor, A.J., Van Petten, C., 2006. Source memory retrieval is affected by aging and prefrontal lesions: behavioral and ERP evidence. *Brain Res.* 1107, 161–176.
- Thompson-Schill, S.L., D'Esposito, M., Aguirre, G.K., Farah, M.J., 1997. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc. Natl. Acad. Sci. U.S.A.* 94, 14792–14797.
- Trott, C.T., Friedman, D., Ritter, W., Fabiani, M., 1997. Item and source memory: differential age effects revealed by event-related potentials. *Neuroreport* 8, 3373–3378.
- Trott, C.T., Friedman, D., Ritter, W., Fabiani, M., Snodgrass, J.G., 1999. Episodic priming and memory for temporal source: event-related potentials reveal age-related differences in prefrontal functioning. *Psychol. Aging* 14, 390–413.
- Tulving, E., Kapur, S., Craik, F.I.M., Moscovitch, M., Houle, S., 1994. Hemispheric encoding/retrieval asymmetry in episodic memory: positron emission tomography studies. *Proc. Natl. Acad. Sci.* 91, 2016–2020.
- Wagner, A.D., Pare-Blagoev, E.J., Clark, J., Poldrack, R.A., 2001. Recovering meaning: left prefrontal cortex guides controlled semantic retrieval. *Neuron* 31, 329–338.
- Watt, N.F., 1976. Two factor index of social position: Amherst modification. An adaptation of Hollingshead and Redlich, 1958. Unpublished manuscript.
- Wegesin, D.J., Friedman, D., Varughese, N., Stern, Y., 2002. Age-related changes in source memory retrieval: an ERP replication and extension. *Brain Res. Cogn. Brain Res.* 13, 323–338.
- West, R.L., 1996. An application of prefrontal cortex theory to cognitive aging. *Psychol. Bull.* 120, 272–292.
- Wilding, E.L., Rugg, M.D., 1996. An event-related potential study of recognition memory with and without retrieval of source. *Brain* 119 (Pt 3), 889–905.
- Wilson, R.S., Bennett, D.A., Gilley, D.W., Beckett, L.A., Barnes, L.L., Evans, D.A., 2000. Premorbid reading activity and patterns of cognitive decline in Alzheimer disease. *Arch. Neurol.* 57, 1718–1723.
- Wilson, R.S., Barnes, L.L., Bennett, D.A., 2003. Assessment of lifetime participation in cognitively stimulating activities. *J. Clin. Exp. Neuropsychol. (Neuropsychol. Dev. Cogn. Section A)* 25, 634–642.
- Yevgenia, K., Elizabeth, G., 2003. Adult neurogenesis: a mechanism for brain repair? *J. Clin. Ex. Neuropsychol. (Neuropsychol., Dev. Cogn. Section A)* 25, 721–732.