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The Relation Between Brain Activity During Memory Tasks and Years of Education in Young and Older Adults

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Higher education is associated with less age-related decline in cognitive function, but the mechanism of this protective effect is unknown. The authors examined the effect of age on the relation between education and brain activity by correlating years of education with activity measured using functional MRI during memory tasks in young and older adults. In young adults, education was negatively correlated with frontal activity, whereas in older adults, education was positively correlated with frontal activity. Medial temporal activity was associated with more education in young adults but less education in older adults. This suggests that the frontal cortex is engaged by older adults, particularly by the highly educated, as an alternative network that may be engaged to aid cognitive function.

Keywords: memory, aging, frontal lobes, encoding, recognition

Old age is associated with a loss of memory function. In particular, older adults have difficulty recollecting personally experienced events, that is, episodic remembering (for a review, see Craik & Bosman, 1992). This deficit may arise from problems in retrieving studied items especially when an effortful search of memory is required (Craik & McDowd, 1987; Macht & Buschke, 1983). Indeed, past studies have shown that age-related loss in episodic memory is larger on tests of recall than of recognition (Craik & McDowd, 1987; Park, Puglisi, & Smith, 1986; Rabinowitz, 1984). Memory loss in older adults also could be caused by an inability to effectively encode new information. Potential sources of this failing are secondary impairments in attention (Craik, 1983, 1986) and information processing (Salthouse, 1996) as well as a heightened susceptibility to interference (Hasher & Zacks, 1988; Winocur & Moscovitch, 1983).

Accompanying the reduced episodic memory in older adults are alterations in neural activity compared with the young. For instance, in a study by Grady et al. (1995), memorization of faces produced less activity in the right hippocampal, left inferior prefrontal, and temporal cortices in an older group compared with a group of young adults. A reduction in the spatial extent of left frontal activity in older adults also has been observed during the encoding of words (Stebbins et al., 2002). However, older adults sometimes have increased right frontal activity during encoding compared with young adults (Rosen et al., 2002). Similarly, retrieval has been associated typically with right frontal activity in young adults but a recruitment of both right and left frontal regions in older adults (Backman et al., 1997; Grady, Bernstein, Siegenthaler, & Beig, 2002; Madden et al., 1999). This consistent demonstration of bilateral activity in frontal regions during retrieval in older adults compared with typically right-lateralized frontal recruitment in the young has led to the suggestion that aging is associated with a reduction in hemispheric asymmetry (HAROLD; Cabeza, 2002). This pattern of bilateral frontal activity during retrieval has occurred in conjunction with poorer face memory (Grady et al., 2002), word recognition (Madden et al., 1999), and cued recall (Backman et al., 1997) in older adults compared with young adults. However, others have reported bilateral frontal activity during memory tasks in which older adults were performing as well as young adults (Cabeza, 2002; Cabeza, Grady, et al., 1997), or in those with better performance among the older adults (Rosen et al., 2002). Thus, although the evidence suggests that in some cases recruitment of frontal areas aids memory performance in older adults, it is still unclear whether such recruitment is generally beneficial to memory ability.

Involvement of medial temporal regions also is frequently found in memory tasks and has been associated with enhanced cognitive ability in both young and older adults. In one study (Schacter, Alpert, Savage, Rauch, & Albert, 1996), words that had been semantically encoded (deep encoding trials) were recalled with higher accuracy and more right hippocampal activity than words that had been learned by attending to their perceptual features (shallow encoding trials). In addition to its benefits during recall, bilateral medial temporal activation was reported to be greater during the encoding conditions that produced the highest recognition scores in both young and older adults, namely intentional and semantic encoding of pictures (Grady, McIntosh, Rajah, Beig, & Craik, 1999). More recently, several studies have reported that hippocampal activity during encoding is correlated directly with better memory performance in both young and older adults (Della-

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Maggiore et al., 2000; Grady, McIntosh, & Craik, 2003; Morcom, Good, Frackowiak, & Rugg, 2003). These results suggest that the participation of medial temporal regions facilitates memory regardless of age.

One factor that is known to account for some of the variance in cognitive ability among older adults, and which may account for variability in brain activity as well, is years of education. Fewer years of education have been associated with a faster age-related decline in memory (Colsher & Wallace, 1991; Evans et al., 1993), mental status (Lyketsos, Chen, & Anthony, 1999; Starr, Deary, Inch, Cross, & MacLennan, 1997), and verbal ability (Arbuckle, Maag, Pushkar, & Chaikelson, 1998; Christensen et al., 1997). Greater education also has an impact on the expression of cognitive deficits in patients with dementia. For example, several studies (Alexander et al., 1997; Stern, Alexander, Prohovnik, & Mayeux, 1992) have reported greater metabolic deficits in parietal regions in more highly educated Alzheimer's patients compared with their less educated peers despite no differences in cognitive ability. That is, more educated patients who are at a later stage of the disease in terms of metabolic deficit display the same level of cognitive ability as less educated patients who are at an earlier stage of the disease. In essence, education does not delay the progression of the Alzheimer's pathology, but it may enhance the ability of the patient to compensate for that pathology. In addition, Bennett et al. (2003) recently examined the effects of formal education on the degree of cognitive decline prior to death and the pathology seen at autopsy in patients with Alzheimer's disease. These authors concluded that education provides a type of cognitive reserve that reduces the deleterious effect of Alzheimer-type pathology on cognitive abilities.

The mechanism by which education is able to retard cognitive decline is not known. The more rapid deterioration in cognitive ability in less educated older adults may result from an inability to recruit the brain regions that underlie effective performance of the cognitive task. Alternatively, the engagement of a compensatory network in more highly educated older adults may account for the preservation of function in these individuals. One suggestion is that individuals differing in education vary in the strategies used to perform a task or in the brain regions underlying their behavior (Stern, Albert, Tang, & Tsai, 1999). That is, education enables the older adult to engage neural circuits that benefit his or her cognitive performance when the brain regions that normally mediate the task no longer function as a cohesive unit. Some evidence for this has been reported recently in an experiment that examined brain activity during the encoding and recognition of nonverbal shapes in young and older adults who were matched in performance level (Scarmeas et al., 2003). In that study, a composite measure derived from education and IQ scores was associated with greater activity in the left cuneus for older adults but in the right inferior temporal and postcentral gyri in young adults. The authors interpreted this finding as evidence of compensatory activity in the older group, reflecting differential success in coping with age-related changes in cognition.

The present study was conducted to explore the relation between education and brain activity during verbal episodic memory and how this relation may change with age. We used functional MRI (fMRI) to measure brain activity in young and older adults during memory tasks and identified the network of brain regions whose activity was correlated with years of education. We also examined how activity in these brain networks was related to accuracy of recognition performance. This approach offered the advantage of examining differences in the relationship between educational attainment and neural activity in young and older populations and how these differences affected memory ability. Consistent with the work reviewed above, we expected that hippocampal activity may be related to recognition in both groups, whereas the use of prefrontal cortices would be correlated with recognition accuracy and educational attainment in older adults but not necessarily in younger adults. That is, if frontal regions are responsible for processes that can be used by older adults to maintain cognitive function, such as organizing, manipulating, and monitoring information (e.g., D'Esposito et al., 1995; Moscovitch, 1992; Shimamura, 1995; Stuss & Benson, 1987), then activity in these areas should be related to education and perhaps also to task performance. Indeed, there is some evidence to support the idea that frontal activity is related to better memory performance in older adults (Cabeza, Anderson, Locantore, & McIntosh, 2002; Grady, McIntosh, & Craik, 2003). However, the evidence on the relation between frontal activity and memory performance in young adults is mixed. Some studies have found that frontal activity during encoding is associated with better performance (e.g., Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Wagner et al., 1998), whereas others have found the opposite (Otten & Rugg, 2001b). Frontal activity during retrieval also has been associated with poorer memory performance in young adults (Grady, McIntosh, Beig, & Craik, 2001). One possible explanation for the variability between studies could be that specific regions within the prefrontal cortex are differently related to memory ability in young adults. That is, activity in inferior prefrontal regions has been associated with better memory (Brewer et al., 1998; Wagner et al., 1998), whereas activity in anterior (Grady et al., 2001) and dorsolateral (Grady, McIntosh, & Craik, 2003) areas has been correlated with poorer memory performance in the young. Therefore, we expected that the networks supporting memory performance as well as those related to education would be different between the groups.

Method

Participants

Twenty-one young adults (between 18 and 30 years of age) participated in the study, but some had to be excluded because of excessive motion during scanning ($n = 5$), failure to normalize properly to the template (see below, $n = 1$), or absence of accuracy data because of problems with the response collection device ($n = 1$). Twenty-nine older adults (65 years of age and older) participated, but some had to be excluded because of excessive motion ($n = 3$), failure to normalize properly to the template ($n = 4$), absence of accuracy data because of problems with the response collection device ($n = 2$), or incomplete fMRI data collection ($n = 1$). The final sample consisted of 14 right-handed young adults (7 men and 7 women, mean age $\pm$ $SD = 23.4 \pm 2.3$) and 19 right-handed older adults (9 men and 10 women, mean age $\pm$ $SD = 73.9 \pm 6.2$). Table 1 shows how the young and older adults compare on several cognitive measures. The more educated young participants consisted of graduate and undergraduate students attending the University of Toronto, Ontario, Canada. The less educated young adults were recruited from the community, as were all of the older adults. The range of educational attainment in the young group was from 11 to 20 years and from 8 to 21 years in the older group. The mean level of education did not differ between the groups, $t(31) = -0.528$, $p = .60$. Structural MRI scans were obtained at the same time as the

Table 1
Demographic Data

Participant parameters	Young adults	Older adults
Age (years)	23.4 (2.3)	73.9 (6.2)
Education (years)	14.7 (3.1)	14.0 (4.7)
HVLT Immediate Recall	8.7 (1.6)	6.4 (1.5)
HVLT Delayed Recall	9.0 (2.0)	6.4 (2.0)
HVLT Recognition	11.0 (1.3)	9.2 (2.0)
WAIS Vocabulary	37.8 (12.9)	48.6 (13.1)
WAIS Information	15.4 (5.1)	20.2 (4.3)
Digit Symbol	82.8 (15.2)	57.8 (15.7)
MMSE	27.8 (2.5)	28.2 (2.3)

Note. Values are means, with standard deviations in parentheses. Significant differences were found between the groups on HVLT (Hopkins Verbal Learning Test; Shapiro, Benedict, Schretlen, & Brandt, 1999) Immediate Recall, $F(1, 31) = 17.5$, $p < .001$; HVLT Delayed Recall, $F(1, 31) = 14.9$, $p = .001$; HVLT Recognition, $F(1, 31) = 9.0$, $p < .01$, WAIS Vocabulary, $F(1, 31) = 5.6$, $p < .05$; WAIS Information, $F(1, 31) = 8.2$, $p < .01$; and WAIS Digit Symbol, $F(1, 31) = 21.0$, $p < .001$. WAIS = Wechsler Adult Intelligence Scale; MMSE = Mini-Mental State Examination.

functional scans to screen out participants who had overt brain abnormalities. None of the participants took medications that might affect brain function. The Ethics Committees of Baycrest Centre for Geriatric Care and Sunnybrook and Women's College Health Science Centre approved this experiment, and each participant gave informed consent.

Stimulus Materials

The stimuli used in the experiment included black line drawings of nameable objects and words corresponding to the names of objects (Snodgrass & Vanderwart, 1980) presented on a white background. Two lists of objects and two lists of words were assigned to the encoding tasks in a counterbalanced fashion. The object lists were matched in terms of the familiarity and the complexity of the line drawings contained within each. *Familiarity* refers to how often people come in contact with an object, and complexity is a measure of the intricacy of the line drawing (Snodgrass & Vanderwart, 1980). The word lists were equated for the frequency of the words in the English language and the word length (Kučera & Francis, 1967).

Procedure

Participants lay supine on the MRI scanner bed, with their head stabilized by an air-filled vacuum cushion. The stimuli were projected from the computer located outside of the scanner room onto a mirror inside the head coil or, for participants needing correctional lenses, through Silent Vision Goggles (Avotec, Stuart, FL) placed over the participants' eyes. During six fMRI runs, participants were engaged in four encoding and two recognition conditions. Two different encoding tasks were performed on words and pictures to facilitate comparison with other studies of aging and episodic memory (e.g., Grady et al., 1999, 2002; Schacter et al., 1996; Stebbins et al., 2002). In a shallow-encoding condition, participants determined whether the pictures presented were large or small and whether the words were printed in capital letters or lowercase. In a deep-encoding condition, participants judged whether the pictures or words corresponded to living or nonliving entities. The participants pushed one of two buttons with either the right middle or the index finger to indicate their response. The stimulus lists for each encoding condition were divided into blocks of six words or pictures, each presented for a duration of 3 s, with 1 s between stimuli. Following each 24-s stimulus block was a sensorimotor control block of equal duration in which participants pushed a button each time a fixation cross appeared on the screen. Thus, each study list consisted of a total of 24 words or pictures, broken up into four stimulus blocks, alternating with the same number of control blocks. The order of the encoding conditions was counterbalanced across the participants.

Immediately following the four encoding conditions, participants were administered two scanned recognition tests, one for the studied words and the other for the studied pictures. The order in which the tests were given was counterbalanced across participants. Both recognition tests were made up of words written in lowercase letters, including the one for the encoded pictures. This was done so that picture memory would be more similar to that for the studied words because both young and older adults demonstrate superior memory for pictures (Paivio, 1971). Each recognition list consisted of 48 words, 32 of which had been studied in one of the previous encoding conditions (as either a word or a picture), and the remaining 16 consisting of new stimuli that the participant had not encountered during the encoding phase. Participants pressed one of two buttons using either their right middle or their index finger to indicate whether the stimulus was old or new. The test lists were divided into blocks of six stimuli (four old and two new), each presented for a duration of 3 s, with a 1-s interstimulus interval. Blocks consisting of items that had been deeply encoded alternated with blocks containing shallowly processed stimuli. Intervening between these stimulus blocks was the same fixation cross-monitoring task that was used as the control task for the encoding conditions.

Scanning Procedure

Imaging was performed with a 1.5 T whole body MRI scanner, with a standard head coil (CV/i hardware, LX8.3 software; General Electric Medical Systems, Waukesha, WI). During the functional scans, the blood oxygenation-level dependent MRI signal was measured from 26 slices, each of which was 5-mm thick. The imaging sequence was a single shot T2-weighted pulse sequence with spiral readout, offline gridding, and reconstruction (TR = 2,500 ms, TE = 40 ms, flip angle 80°). Structural scans were obtained prior to task performance by using a three-dimensional (3-D) T1-weighted pulse sequence (TR = 12.4 ms, TE = 5.4 ms, flip angle 35°, 22 × 16.5 field of view, 124 axial slices 1.4-mm thick).

Data Analysis

The measure of accuracy on the recognition tests was the proportion of new stimuli that the participant incorrectly identified as old (false alarms) subtracted from the proportion of stimuli that were correctly labeled as old (hits). A repeated-measures analysis of covariance was applied to these data, with stimulus type (words or pictures) and encoding strategy (shallow or deep) as the repeated measures, group as the independent factor, and number of years of education as the covariate.

Motion correction of the images was performed using the software package Analysis of Functional Neuroimages (AFNI; Cox, 1996). Each of the six functional runs for each participant was registered to the single functional run that reduced the amount of movement to less than 1 mm. The first functional run of the encoding tasks was used as the reference for most of the participants. The realigned images were then spatially normalized, using a linear algorithm, to a template that was itself normalized to the brain space of the Montreal, Quebec, Canada, Neurologic Institute and approximates the space of the Talairach atlas (Talairach & Tournoux, 1988). This template was constructed by averaging together the spiral MRI scans of 30 young adults. The normalized images were then smoothed with an 8-mm filter using SPM99 (Frackowiak & Friston, 1994). Mean images for each condition (four encoding and two recognition) for each participant were calculated, resulting in six images per participant. Prior to statistical analysis, the raw value of the signal within each voxel was converted to a ratio by dividing by the average value (averaged across all runs) of all voxels in the participant's brain.

Partial least squares (PLS, McIntosh, 1999) was used to determine the set of brain regions whose activity was correlated with both years of education and recognition accuracy. All of the mean images for the encoding and recognition conditions for both young and older adults were entered into a single analysis. The measure of recognition accuracy was the average proportion of hits–false alarms associated with recognition of the stimuli on both the picture and word recognition tests, regardless of the manner in which the stimuli had been encoded. This overall measure of recognition accuracy was used as an estimate of general memory ability, similar to the way years of education is an estimate of general intellectual function. Both mean recognition accuracy and years of education were entered into the same analysis in order to determine whether there were common brain areas related to both educational level and memory ability and what areas might support memory ability independent of educational attainment. This method of statistical analysis assesses the correlation between the fMRI signal in each brain voxel and the two behavioral variables (Grady, McIntosh, Beig, et al., 2003). These correlations are then contrasted across conditions and groups using singular value decomposition, resulting in a number of latent variables (LVs). Thus, this analysis can identify patterns of brain activity that are the same, or different, across conditions or between groups. Each LV consists of a singular image that depicts the brain regions that correlate with number of years of education (and/or recognition accuracy). Each voxel in the singular image has a numerical weight (salience) that describes how that voxel is related to the behavioral variables. The degree to which each participant expresses the brain pattern depicted in the singular image (brain score) is calculated by multiplying the fMRI images for each participant in each condition by the singular image. These brain scores are similar to factor scores in a factor analysis. The correlation between the brain score of each participant and the behavioral variable (number of years of education or recognition accuracy) is computed for each condition. A positive correlation means that high brain scores (voxels with positive salience) are related to high levels of the behavioral variable (e.g., high education or high recognition accuracy). In contrast, high values of the behavioral variable are related to low brain scores (voxels with negative salience) when the correlation is negative. The reliability of each correlation was determined using a bootstrap estimation of the confidence intervals, using 100 bootstrap samples and a random resampling of the participants, with replacement. The 95% confidence interval was used as the threshold for reliability for these correlations. The bootstrap also was used to determine the reliability of each voxel's salience by calculating the standard error of the saliences. *Reliable voxels* were defined as those possessing a salience:standard error ratio (reliability ratio) greater than or equal to 2.6 (Efron & Tibshirani, 1986), which is equivalent to a 99% confidence limit. Any voxel containing a reliability ratio higher than other voxels within an 8-mm cube radius was considered to be the "peak" voxel (local maxima) for that brain area. The coordinates for these local maxima were expressed as Brodmann's areas (BA) using the Talairach atlas. In addition to the bootstrap procedure, the significance of each LV as a whole was assessed with a permutation test (McIntosh, Bookstein, Haxby, & Grady, 1996) using 500 permutations.

Results

Memory Performance

The young and older adults classified the pictures and words as living/nonliving (deep-encoding condition) and made size judgments (shallow-encoding condition) with high accuracy. The groups did not differ in their accuracy (older $M = 0.89$; young $M = 0.90$), $F(1, 31) = 0.215$, $p > .05$. Hit rates, false alarm rates, and corrected accuracy measures (proportion of hits–proportion of false alarms) are shown in Table 2 for the young and older adults. The significant main effects for recognition accuracy, covarying out the effect of education, included that of group, $F(1, 31) = 11.3$, $p < .01$, and encoding condition, $F(1, 31) = 44.3$, $p < .001$. The young were more accurate than the older adults, and deeply encoded items were remembered better than shallowly encoded items. The Stimulus Type × Encoding Condition interaction was also significant, $F(1, 31) = 6.60$, $p < .05$, indicating that the difference in accuracy resulting from the encoding task was greater for words than for pictures. This was true for both the young and the older adults. The accuracy of recognition (collapsed across stimulus type and encoding task) was not significantly correlated with years of education in either the young or the older adults (young $r = .10$, $p > .05$; older $r = .17$, $p > .05$).

Brain–Behavior Correlations: Education and Recognition Accuracy

The analysis of the relation between brain activity during encoding and recognition with accuracy and years of education resulted in a number of significant LVs. These LVs identified patterns of brain activity that were correlated with education and/or accuracy and that differentiated young from older, but none of the patterns varied across encoding and recognition conditions (the results of analyses carried out on the scans from encoding and recognition separately can be found on the Web at http://dx.doi.org/10.1037/0894-4105.19.2.181.supp). The first LV in the combined group analysis of the correlation between brain activity, years of education, and recognition accuracy (permutation $p < .01$, Figure 1; for color versions of the

Table 2
Accuracy of Picture and Word Recognition

Measure	Pictures: Young	Pictures: Older	Words: Young	Words: Older
		Shallow		
Hits − false alarms	0.43 ± 0.16	0.32 ± 0.30	0.35 ± 0.29	0.20 ± 0.23
Hits	0.58 ± 0.15	0.46 ± 0.21	0.45 ± 0.22	0.34 ± 0.19
False alarms	0.14 ± 0.11	0.14 ± 0.14	0.10 ± 0.10	0.13 ± 0.13
		Deep		
Hits − false alarms	0.62 ± 0.17	0.43 ± 0.25	0.76 ± 0.17	0.49 ± 0.29
Hits	0.71 ± 0.12	0.59 ± 0.17	0.85 ± 0.15	0.58 ± 0.24
False alarms	0.10 ± 0.10	0.16 ± 0.19	0.09 ± 0.09	0.09 ± 0.14

Note. Values for each condition are the mean ± standard deviation.

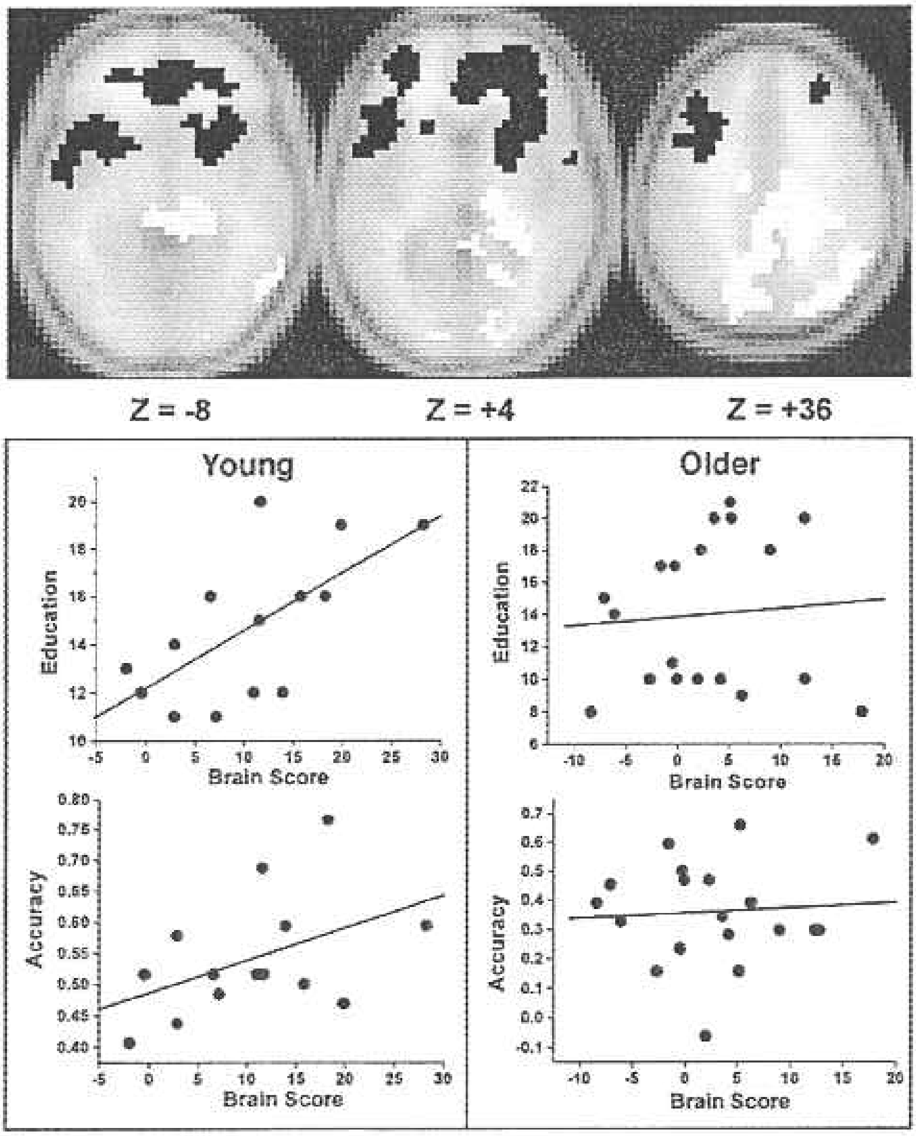

Figure 1. Brain areas in which activity during the encoding and recognition tasks was correlated with recognition accuracy and years of education in young adults are shown in the top of the figure. In this figure, and in all subsequent figures, activated areas are shown on a standard average magnetic resonance image (from SPM99) at the indicated level in millimeters relative to the anterior–posterior commissure line. The right side of the image corresponds to the right side of the brain, and the left side of the image corresponds to the left side of the brain. Activity in the regions shown in white were positively correlated with high education and high accuracy, and those shown in black had negative correlations. The maxima for these regions can be found in Table 3. The bottom of the figure shows the correlations between mean brain score (averaged over all task conditions) and the external variables for the young and older participants. The mean brain score was used because individual scores did not vary appreciably across the task conditions. These graphs indicate that increasing activity in the white areas and, hence, increasing brain scores were associated with more years of education ($r = .66$) and better recognition accuracy ($r = .46$) in the young adults. Conversely, increasing activity in the black areas and, hence, decreasing brain scores were associated with fewer years of education and poorer recognition accuracy. The correlations in older adults were not reliable ($rs = .08$ and .07 for education and recognition, respectively). A color version of this figure is on the Web at http://dx.doi.org/10.1037/0894-4105.19.2.181.supp.

figures, see the supplementary material on the Web at http://dx.doi.org/10.1037/0894-4105.19.2.181.supp) characterized the young adults. The brain pattern consisted of a set of regions in which activity during encoding and recognition was correlated reliably with the educational attainment of the young adults and their accuracy of recognition (rs between brain scores and behavioral variables range from 0.44 to 0.67). In the older adults, this pattern of brain activity was not reliably correlated with educational attainment or recognition accuracy. A higher level of education and greater recognition accuracy in the young was associated with activity in mostly posterior areas such as the posterior cingulate gyrus, cuneus and precuneus, and lateral and medial temporal regions (see Figure 1 and Table 3). Fewer years of education and poorer recognition performance in the young was correlated with activity in mostly anterior regions, including the prefrontal cortex bilaterally (although more prominent in the left hemisphere), premotor regions, and the temporal pole in the left hemisphere (see Figure 1 and Table 3). Thus, this LV revealed a common set of brain regions in which activity was related to both the educational attainment and the recognition memory of young adults across all the tasks. Prefrontal activity was associated with poorer recognition and less education, and posterior temporoparietal activity was associated with better recognition and more education.

The second LV (permutation $p < .01$) identified a group of brain regions in which activity during the memory tasks was correlated with level of education in the older adults (range of r values in older adults = 0.53–0.59). This pattern of brain activity was not reliably correlated with recognition accuracy in older adults. The correlations between education and brain activity in the young adults were opposite of that seen in the older group (see Figure 2), although neither these nor the correlations with accuracy were reliable in this group. More years of education in the older adults were correlated with activity in right-lateralized areas of the temporal and parietal cortices and cingulate gyrus (see Figure 2 and Table 4). Prefrontal areas also showed this pattern of correlations bilaterally but more extensively in the right hemisphere. In contrast, lower educational attainment in the older adults was associated with activity in the postcentral gyrus and the lingual gyrus in the left hemisphere and in inferior and medial portions of the left temporal lobe, including the parahippocampal gyrus (see Figure 2 and Table 4).

A third LV (permutation $p < .01$, Figure 3) identified a set of brain areas whose activity was correlated only with recognition accuracy in the older adults (range of r values = 0.73–0.75). This group of brain regions was not reliably correlated with education in older adults or with years of education or recognition accuracy in young adults (although again, the correlations in young and older adults were in opposite directions; see Figure 3). More accurate recognition of the study items in older adults was associated with activity in the left premotor cortex, right lingual gyrus, and left caudate nucleus. Poor memory for the study items was related to activity in premotor regions bilaterally, the middle temporal cortex in both hemispheres, and foci within the right and left parietal cortices (see Table 5 and Figure 3). However, the area most strongly correlated with poorer memory performance in older adults was a region of the left anterior medial temporal cortex.

To summarize these results, young adults showed overlap in those brain networks that were associated with education and recognition ability, whereas these networks were dissociated in older adults. Increasing activity in posterior brain regions was correlated with more education and better accuracy in younger adults, whereas increasing activity in frontal areas was correlated with less education and poorer accuracy in this group. Conversely, bilateral frontal activity was associated with more education in the older group, as was right temporal activity. Positive correlations

Table 3

Local Maxima of Areas Where Activity Is Correlated With Level of Education and Recognition Accuracy in Young Adults

Region	Hem	BA	X	Y	Z	Sal/SE
Positive correlations						
Motor						
GPrC	R	4	4	−32	68	6.1
GPrC	L	4	−4	−44	64	7.7
Cingulate	R	23	8	−20	32	11.1
	L	23	−12	−16	32	7.6
Temporal						
GH	R	36	20	−24	20	3.6
GTm	R	39	28	−64	16	4.6
GTs	L	42	−28	−32	20	4.3
Parietal						
GPoC	R	3,1,2	24	32	60	6.8
GMs	R	40	48	56	36	7.3
LPs	L	7	16	40	60	7.3
Pcu	R	7	24	−68	44	5.3
Occipital						
Cu	R	31	16	−60	8	4.6
Cu	L	18	12	−88	12	4.4
GOs	R	19	36	−76	32	7.6
GF	R	37	56	−64	−12	4.2
Thalamus	R		16	−20	8	8.2
Midbrain	R		4	−28	−8	6.6
Negative correlations						
Prefrontal						
GFi	L	45	52	32	20	6.9
GFm	L	10	28	48	20	5.3
GFm	R	10	32	48	24	6.6
GFs	R	8	8	44	44	3.7
GFs	L	8	−16	28	56	3.8
GFd	R	11	4	48	−12	5.8
Premotor						
GPrC	R	6	56	4	12	7.1
GPrC	L	6	−48	0	24	3.7
Cingulate	R	24	8	40	8	5.3
Temporal						
GTs	L	22	−48	12	−4	5.2
GTm	L	21	−44	−24	−4	2.7
Putamen	R		20	4	4	5.7

Note. Areas in the table were identified by the first latent variable (LV) in the behavioral analysis. Coordinates and estimated Brodmann's areas (BA) are from the Montreal Neurological Institute template in SPM99 and are similar to the coordinates from Talairach and Tournoux (1988). X (R/L) = negative values are in the left hemisphere (Hem); Y (anterior–posterior) = negative values are posterior to the zero point (located at the anterior commissure); Z (superior–inferior) = negative values are inferior to the plane defined by the anterior and posterior commissures; Sal/SE = reliability ratio for each region on this LV; Cu = cuneus; GF = fusiform gyrus; GF(i, m, s, d) = frontal gyrus (inferior, middle, superior, medial); GH = parahippocampal gyrus; GMs = supramarginal gyrus; GOs = superior occipital gyrus; GPoC = postcentral gyrus; GPrC = precentral gyrus; GT(m, s) = temporal gyrus (middle, superior); LPs = superior parietal; Pcu = precuneus.

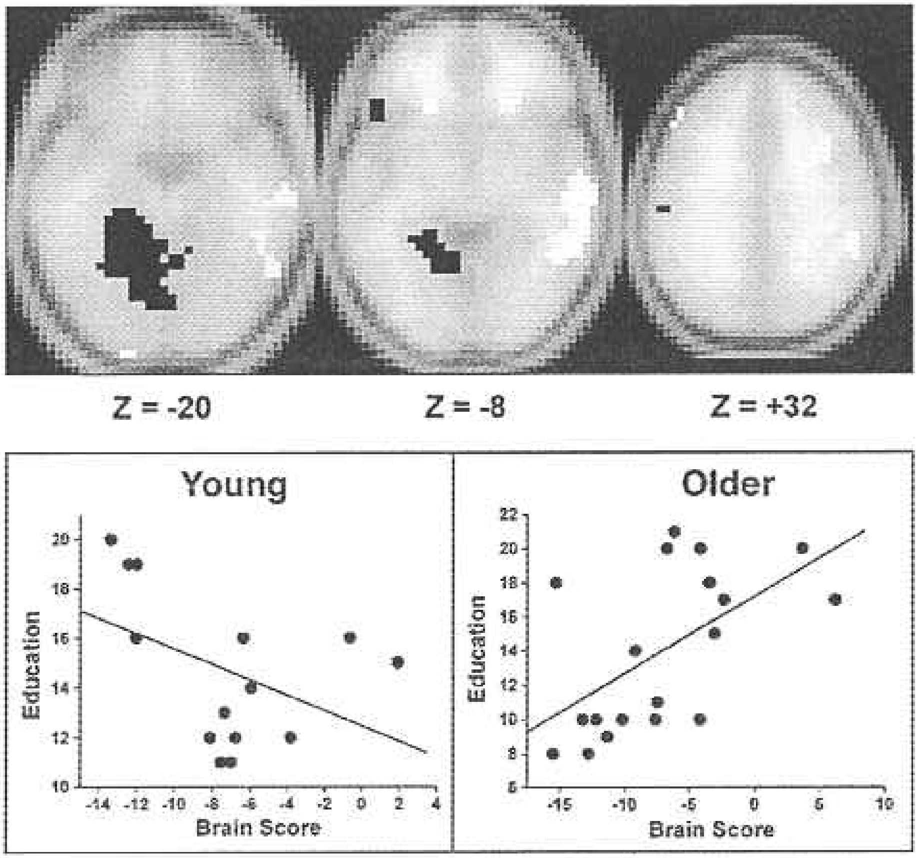

Figure 2. Brain areas in which activity was correlated with years of education in older adults are shown in the top of the figure. Activity in the regions shown in white was correlated with high education in older adults. Activity in the regions shown in black was associated with low education in older adults. These correlations are depicted in the bottom half of the figure, which shows the correlations between mean brain scores and years of education for the young ($r = -.44$) and older participants ($r = .57$). The maxima for the correlated areas can be found in Table 4. A color version of this figure is on the Web at http://dx.doi.org/10.1037/0894-4105.19.2.181.supp.

between recognition and brain activity in older adults were seen in only a few regions, including caudate and left motor cortex. Activity in medial temporal regions also distinguished the groups. In young adults, activity in the medial temporal cortex was generally associated with both more education and better recognition, whereas in older adults, medial temporal activity was associated with less education (posterior regions) and poorer performance (anterior regions).

Discussion

The behavioral data from this experiment concur with previous reports concerning recognition memory in young and older adults. The older adults recognized fewer stimuli than did the young adults, which adds to other evidence for deficits in recognition memory that occur with age (Craik & Jennings, 1992). Moreover, the memory of both the young and older adults was superior following semantic encoding of the pictures and words compared with processing the perceptual aspects of the stimuli. This finding replicates considerable previous work on the levels of processing effect and the robust nature of this effect regardless of age (Craik & Simon, 1980; Craik & Tulving, 1975). This benefit for memory of deep encoding over shallow processing was greater when stimuli were initially encoded as words than when pictures were studied, which is consistent with other investigations of recognition memory (Grady et al., 2001; Grady, McIntosh, Rajah, & Craik, 1998).

The main finding from this experiment, and its novel contribution, is that the brain regions associated with years of education and overall memory ability differ with age. We found that the brain networks related to both years of education and memory performance either showed no overlap between young and older adults or were inversely related. That is, the multivariate analysis used here identified a pattern of brain activity characterizing education and performance in young adults that was orthogonal to those showing these relations in older adults. Such divergence of brain networks with age has been shown previously (Cabeza, McIntosh,

Table 4
Local Maxima of Areas Where Activity Is Correlated With Level of Education in Older Adults

Region	Hem	BA	X	Y	Z	Sal/SE
Positive correlations in older adults						
Prefrontal						
GFm	R	9	32	16	32	3.3
GFm	L	46	−52	32	28	4.0
GFs	L	6	−24	12	64	4.6
Cingulate	R	32	20	28	−8	4.2
Parietal						
LPi	R	40	52	−40	36	3.1
Temporal						
GTm	R	21	52	−44	−8	4.1
GTi	R	20	64	−20	−20	3.7
Negative correlations in older adults						
Parietal						
GPoC	L	3.1.2	−36	40	64	3.4
Temporal						
GTi	L	20	−48	0	−36	4.3
GPoC	L	3.1.2	−56	−20	28	3.2
GH	L	36	12	40	0	5.0
Occipital						
GF	L	37	−24	−44	−16	5.1
GL	L	18	−20	−68	4	3.2

Note. Areas in the table were identified by the second latent variable (LV) in the behavioral analysis. Coordinates and estimated Brodmann's areas (BA) are from the Montreal Neurological Template in SPM99. X (R/L) = negative values are in the left hemisphere (Hem); Y (anterior posterior) = negative values are posterior to the zero point (located at the anterior commissure); Z (superior inferior) = negative values are inferior to the plane defined by the anterior and posterior commissures; Sal/SE = reliability ratio for each region on this LV; GF (m, s) = frontal gyrus (middle, superior); LPi = inferior parietal; GTm = middle temporal gyrus; GTi = inferior temporal; GPoC = postcentral gyrus; GH = parahippocampal gyrus; GF = fusiform gyrus; GL = lingual gyrus.

Tulving, Nyberg, & Grady, 1997; Della-Maggiore et al., 2000; Grady et al., 2002; Grady, McIntosh, & Craik, 2003), and the results of this experiment extend this finding to the correlation of brain activity during memory encoding and retrieval with years of education. Some researchers have suggested that the reorganization of brain function in older adults may be a type of cognitive reserve that would be associated with more education and maintained cognitive function into old age (Stern, 2002). The results of the present study would be consistent with this notion of cognitive reserve, as an age-related and perhaps compensatory alteration in the neural networks engaged during cognition in those individuals with higher education.

In young adults, we found a network of regions in which activity during encoding and recognition was strongly related to both years of education and performance on the recognition tasks. Specifically, an increase of activity in widespread areas of the frontal cortex was associated with less education in the young. These areas included left inferior frontal gyri, bilateral middle frontal cortices, bilateral superior frontal gyri, and the premotor cortex bilaterally. The recruitment of these frontal regions also was greater in the more poorly performing young adults. By contrast, their more educated peers engaged posterior areas that also were correlated with better recognition memory. At first glance, these data may seem contradictory to published reports that activity in the inferior frontal gyrus improves subsequent memory for specific studied items (Brewer et al., 1998; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Otten & Rugg, 2001a; Wagner et al., 1998). However, there are important differences between those studies and the present one. The previous experiments examined the relation between activity at encoding and how this differentiated items that were subsequently remembered or not. Our study did not examine the relationship between brain activity during the encoding of particular items and the later ability to remember them. Rather, we determined how activity in specific brain areas was associated with individual differences in overall recognition memory, and these correlations were the same across both encoding and recognition conditions. Using a similar analytic technique, other investigators have found an association between frontal activity and poorer recognition memory in the young. For example, Grady et al. (2001) used a similar experimental paradigm with positron emission tomography and found that young adults who remembered fewer stimuli demonstrated greater activity in bilateral frontal cortex. In that study, the investigators proposed that involvement of frontal regions is greatest in young adults who are exerting more effort in recognizing the stimuli. The results of the present investigation are in line with this explanation. An interesting parallel to these findings is a study by Smith et al. (2001) involving task-switching in working memory. The requirement to switch between the performance of two different tasks resulted in extensive activity in the prefrontal cortex for older adults and poor performing young adults, but not for young adults who performed well on the task. Similar findings have been reported (Rypma & D'Esposito, 2000) for a working memory task in which recruitment of the dorsolateral prefrontal cortex was associated with poorer performance in a young group (as indexed by slower reaction time). Taken together, these data suggest that young adults who are challenged by a cognitive task, and consequently perform worse, engage the frontal cortex to a greater degree. Our finding of a similar relation between increased frontal activity and less education indicates that those young individuals with less education may also tend to be those who expend greater effort on cognitive tasks, although there was not a significant correlation between years of education and recognition performance on the specific tasks used here.

The relationship between brain activity and years of education in the older adults was quite different from that seen in the young, most notably in that bilateral dorsolateral frontal regions were engaged more by the highly educated older adults during encoding and recognition. This correlation between frontal activity and education in older adults is consistent with the numerous studies that have found increased prefrontal activity in older compared with younger adults (for a review, see Cabeza, 2002) and indeed could be a partial explanation for this common finding. That is, higher educated and healthier older adults are typically recruited for functional neuroimaging experiments, and it is these individuals who may be more likely to engage frontal areas during memory tasks, as is often observed. The relation between frontal activity and education in older populations also is consistent with the hypothesis that recruitment of this area of cortex, particularly in dorsolateral areas, facilitates cognitive function and thus may play a compensatory role (e.g., Cabeza, 2002; Grady, McIntosh, &

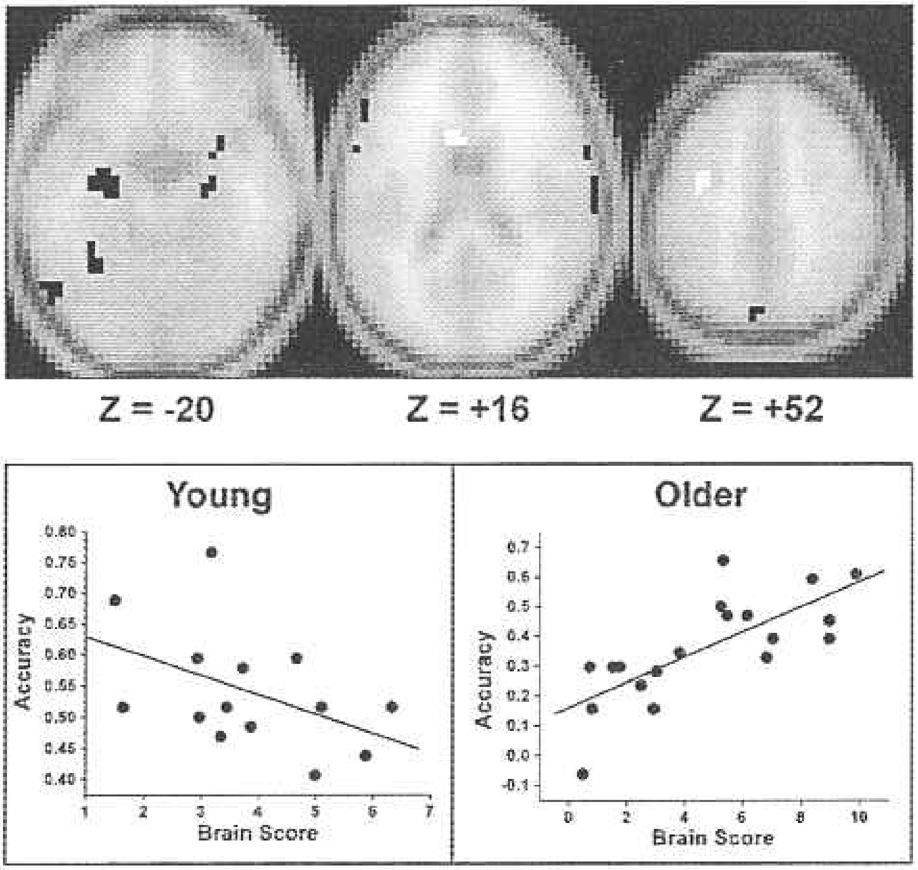

Figure 3. Brain areas in which activity was correlated with recognition accuracy in older adults are shown in the top of the figure. Activity in the regions shown in white was correlated with high recognition accuracy in older adults. Activity in the regions shown in black was associated with low-recognition accuracy in older adults. These correlations are depicted in the bottom half of the figure, which shows the correlations between mean brain score and recognition accuracy for the young ($r = -.46$) and older participants ($r = .74$). The maxima for the correlated areas can be found in Table 5. A color version of this figure is on the Web at http://dx.doi.org/10.1037/0894-4105.19.2.181.supp

Craik, 2003). However, there was no evidence in the present experiment that the frontal regions recruited by the highly educated older adults during encoding and retrieval directly improved their ability to recognize the study items. In fact, there were two distinct brain patterns that were correlated with recognition accuracy and with years of education in the older adults. In addition to the absence of an association between frontal activity and recognition accuracy, there was no evidence that the more educated older adults had significantly better recognition memory on these tasks than did their less educated peers. Despite the lack of an association between activity in the dorsolateral prefrontal cortex and performance on this recognition memory task in the older adults, such associations have been reported previously (Grady et al., 2002; Grady, McIntosh, & Craik, 2003; Rypma & D'Esposito, 2000). Thus, it is possible that this area has a general compensatory function that, when engaged, can facilitate a variety of cognitive processes but may or may not affect task accuracy directly, consistent with the proposed role of frontal regions in executive functions (e.g., Stuss & Benson, 1987). This interpretation is consistent with an earlier study (McIntosh, Rajah, & Lobaugh, 1999) that reported a differential pattern of brain activity in a functionally related set of brain regions, including the left dorsolateral prefrontal cortex, only in participants who were aware of the stimulus contingencies inherent in the task paradigm (i.e., that a particular auditory stimulus presentation predicted presentation of a visual stimulus). However, activity in the prefrontal cortex per se was not related to performance on the task, as we found here, suggesting that this area is involved in general monitoring functions, one of which may be the process whereby sensory input and behavioral responses enter into awareness. Regardless, our data clearly show that prefrontal function is related differently to education in young and older adults and hence, may differentially mediate those cognitive functions related to education.

In addition to the frontal cortex, medial temporal regions also showed age differences in how activity was related to education and recognition accuracy. Young adults showed a positive corre-

Table 5

Local Maxima of Areas Where Activity Is Correlated With Recognition Accuracy in Older Adults

Region	Hem	BA	X	Y	Z	Sal/SE
Positive correlations						
Motor, GPrC	L	4.6	−32	−8	56	3.2
Occipital, GL	R	19	32	−52	−4	3.1
Caudate	L		−12	12	20	3.5
Negative correlations						
Premotor						
GPrC	R	6	60	12	8	3.8
GPrC	L	6	−56	−8	40	2.9
Prefrontal, GFi	L	44	−60	8	20	3.7
Temporal						
GTm	R	21	36	12	28	4.9
GTs	L	22	−64	−56	16	3.6
GH	L	28	−32	8	24	8.3
Parietal						
GPoC	R	43	64	16	20	5.0
LPs	L	7	−8	72	56	3.4
LPs	R	7	32	−48	68	3.4

Note. Areas in the table were identified by the fourth latent variable (LV) in the behavioral analysis. Coordinates and estimated Brodmann's areas (BA) are from the Montreal Neurological Institute Template in SPM99. X (R/L) = negative values are in the left hemisphere (Hem); Y (anterior/posterior) = negative values are posterior to the zero point (located at the anterior commissure); Z (superior/inferior) = negative values are inferior to the plane defined by the anterior and posterior commissures; Sal/SE = reliability ratio for each region on this LV; GPrC = precentral gyrus; GL = lingual gyrus; GFi = inferior frontal gyrus; GT (m, s) = temporal gyrus (middle, superior); GH = parahippocampal gyrus; GPoC = postcentral gyrus; LPs = superior parietal.

lation between medial temporal activity, education and better performance in the first LV, in the right hemisphere. This is consistent with other literature showing that activity in this area supports memory in younger individuals (e.g., Brewer et al., 1998; Grady, McIntosh, & Craik, 2003). In contrast, engagement of posterior medial temporal areas was seen in the less educated older adults, and activity in anterior regions was found in those with poorer memory ability. The anterior medial temporal area associated with poor recognition accuracy in older adults has recently been identified as signaling stimulus familiarity (Brown & Aggleton, 2001; Henson, Cansino, Herron, Robb, & Rugg, 2003) such that novel items produce a greater response in this area than previously seen stimuli. The association of activity in these regions with poor recognition memory in older adults suggests that the familiarity signal is altered in this group. The association of greater activity with worse performance could indicate that familiar items, rather than novel stimuli, are triggering activity in the anterior medial temporal regions of some older adults. The enhanced response would lead to the incorrect belief that the stimulus was novel, and hence performance would be reduced. These results add to other evidence suggesting that older adults differ in their engagement of medial temporal areas during memory tasks, compared with their younger counterparts (Grady et al., 1995, 1999; Mitchell, Johnson, Raye, & D'Esposito, 2000).

Conclusion

The present study demonstrated a difference in the relationship between brain activity and years of education between young and older adults. In young adults, the same network of regions involved in encoding and retrieval was associated with education and recognition accuracy. Frontal activity occurred in the less educated young and was correlated with poor recognition memory, whereas the more educated young adults and those with better memory performance engaged posterior regions of the brain. Older adults showed separate networks related to education and memory performance, with frontal and lateral temporal regions related to more education but not to performance. Perhaps the most interesting age difference is that the correlation between brain activity at study and at test with years of education is the opposite in the groups in some areas. Frontal regions are used more by highly educated older and less educated young adults, and medial temporal regions are recruited by less educated older and highly educated young adults. These data provide further evidence for an age-related alteration in the regions mediating cognition and suggest that the frontotemporal network engaged by the highly educated older adults may be a type of cognitive reserve or alternative network engaged to aid cognitive performance (Stern, 2002).

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