The Effects of Encoding Task on Age-Related Differences in the Functional Neuroanatomy of Face Memory

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Age-related differences in brain activity mediating face recognition were examined using positron emission tomography. Participants encoded faces using a pleasant–unpleasant judgment, a right–left orientation task, and intentional learning. Scans also were obtained during recognition. Both young and old groups showed signficant effects of encoding task on recognition accuracy, but older adults showed reduced accuracy overall. Increased brain activity in older adults was similar to that seen in young adults during conditions associated with deeper processing, but was reduced during the shallow encoding and recognition conditions. Left prefrontal activity was less in older adults during encoding, but greater during recognition. Differential correlations of brain activity and behavior were found that suggest older adults use unique neural systems to facilitate face memory.

Memory for people's faces is an ability that is required of everyone on a daily basis. In the absence of syndromes, such as prosopagnosia, recognition of faces usually requires little or no conscious effort. However, this ability does change as we get older. Elderly individuals consistently show reductions in recognition memory for unfamiliar faces (Bartlett & Leslie, 1986; Bartlett, Leslie, Tubbs, & Fulton, 1989; Crook & Larrabee, 1992; Smith & Winograd, 1978), whereas recognition of other types of complex visual information, such as pictures of objects or scenes, is often spared or only slightly reduced compared with that of younger adults (Craik & Jennings, 1992; Grady, McIntosh, Rajah, Beig, & Craik, 1999; Park, Puglisi, & Sovacool, 1983; Smith, Park, Cherry, & Berkovsky, 1990). However, despite the wealth of behavioral work over the years that has shown that memory for faces is affected adversely by age, the neural mechanisms of this change remain unclear.

Recently, neuroimaging research on face processing has focused on the idea that a particular region in the brain, known as the fusiform gyrus, is critically involved in face perception and memory (Andreasen et al., 1996; Courtney, Ungerleider, Keil, &

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Correspondence concerning this article should be addressed to Cheryl L. Grady, Rotman Research Institute, Baycrest Centre for Geriatric Care, 3560 Bathurst Street, Toronto, Ontario, Canada M6A 2E1. E-mail: cgrady@rotman-baycrest.on.ca Haxby, 1996, 1997; Haxby et al., 1994, 1996; Kanwisher, McDermott, & Chun, 1997; Kuskowski & Pardo, 1999; McCarthy, Puce, Gore, & Allison, 1997; Moscovitch, Winocur, & Behrmann, 1997; Sergent, Ohta, & MacDonald, 1992). This area shows larger increases in activity for faces than for other kinds of stimuli (Haxby et al., 1999; Kanwisher et al., 1997; Kanwisher, Stanley, & Harris, 1999) and is an important part of the face perception network (Horwitz et al., 1992; McIntosh et al., 1994). The participation of additional brain areas, such as prefrontal and temporal cortices as well as the hippocampus, becomes increasingly more prominent as the delay between the initial presentation of a face and subsequent presentations lengthens, that is, as the demands on memory increase (Courtney et al., 1997; Haxby et al., 1996; Haxby, Ungerleider, Horwitz, Rapoport, & Grady, 1995). From these experiments, it seems clear that a variety of brain areas, along with the fusiform gyrus, can be engaged in tasks involving face processing, depending on the specific task demands.

The neural correlates of face perception and memory in the elderly have not been studied at length, but some interesting age-related differences have been noted. Perceptual mechanisms are largely intact, as evidenced by equivalent measures of accuracy on a facematching task in old adults compared with young adults as well as equivalent activation of cortex in the fusiform gyrus (Grady et al., 1994). However, the older individuals also showed greater activation in prefrontal cortex and increased feedback from prefrontal cortex to occipital regions compared with young adults (Horwitz et al., 1995; McIntosh et al., 1994). The brain areas mediating short-term memory for faces (up to 20 s) also are similar in young and old adults, with both showing increased activity in prefrontal and temporal lobe areas and nearly equivalent memory performance (Grady, McIntosh, Bookstein, et al., 1998). In addition, older adults again had more activation than younger adults did in prefrontal cortex, particularly in the left hemisphere. In contrast, memory for faces over a longer time period (15-20 min) was markedly reduced in older adults, as was the activity in some memory-related brain areas (Grady et al., 1995). Specifically, the older adults showed reduced brain activity in left temporal and prefrontal regions during face encoding and reduced activity in pari-

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etal regions during recognition. However, the young and old groups had equivalent activity in right prefrontal cortex during recognition.

Taken together, these experiments indicate that poor longer term face memory in older adults is associated with reduced activity in the brain regions that presumably mediate task performance, whereas relatively good short-term face memory in the elderly is associated with activity in participating brain areas that is equivalent to that seen in younger individuals. In addition, these experiments raise the issue of brain areas that actually show greater activity in older compared with younger adults. As noted above, left prefrontal cortex was activated more in the older adults during face perception and short-term face memory. Greater activation of left prefrontal cortex in older adults also has been found during verbal memory, using both recognition and cued recall as retrieval tasks (Backman et al., 1997; Cabeza et al., 1997; Madden, Turkington, et al., 1999) and during spatial memory tasks (Reuter-Lorenz et al., 2000). This additional activity has been interpreted as an indication of greater demands on the executive functions of the frontal lobes that may reflect a compensatory mechanism, particularly when there are no age-related reductions in performance (Cabeza et al., 1997; Grady et al., 1994). However, increased prefrontal activity has been found in older adults even when their memory performance is lower than that seen in young adults (Madden, Turkington, et al., 1999), suggesting that recruitment of frontal or other areas may reflect differential use of cognitive resources, but not necessarily compensation.

The purpose of this study was to reexamine the issue of agerelated differences in brain activity during episodic face memory tasks and to explore the effect of different encoding tasks on these differences. We wanted to know whether the reductions previously seen in frontal and temporal regions during encoding and in parietal regions during retrieval would be sensitive to manipulations that improve memory performance. For example, it is possible that the older adults in our original face memory study showed reduced activity during the tasks because they were given standard intentional learning instructions and were unable to come up with a successful encoding strategy on their own (Craik & Byrd, 1982; Hultsch, 1969; Sanders, Murphy, Schmitt, & Walsh, 1980). If older adults engage in some orienting task during encoding that results in better face recognition than that seen following intentional learning instructions, would brain activity in frontal or posterior regions or both increase to levels seen in younger adults? Another possibility is that an encoding task that boosts memory performance might be accompanied by the kind of age-specific increased prefrontal activity that is seen in those memory experiments previously noted. Indeed, these two possibilities are not mutually exclusive. That is, under some conditions, older adults might show activity in memory-related areas that is equivalent to that seen in young adults and show increased activity in other areas in which young adults do not show an increase. To examine these issues, we manipulated the level of performance in young and old adults, using a "levels of processing" approach (Craik & Lockhart, 1972; Craik & Rabinowitz, 1985) and encoding tasks that have been shown to modulate memory for faces (Bower & Karlin, 1974; Smith & Winograd, 1978). In this experiment, we used the "deep" task that has been used typically for faces, which is to judge the pleasantness of the face (Smith & Winograd, 1978), and contrasted this with a perceptual orienting task (right-left orientation) and with intentional learning. From previous work (Smith & Winograd, 1978), we expected that the pleasantness judgment would

result in better face recognition compared with the two other encoding tasks in both age groups. Because we previously found that older adults had reduced activity in critical areas during intentional learning of faces, the contrast of learning and judging pleasantness in this experiment would give us the opportunity to see if a better encoding task resulted in fewer age-related reductions in brain activity. In addition, we reasoned that if recruitment of a given brain area, such as left prefrontal cortex, during face recognition was the result of a compensatory mechanism, this recruitment would most likely be observed in those conditions in which memory performance was best. That is, judgment of a face's pleasantness might be expected to result in fewer age-related reductions in brain activity during encoding, compared with the less efficient encoding tasks, as well as to induce some compensatory-related recruitment during retrieval. Finally, perhaps the strongest evidence for compensation in the older brain would be to find a correlation between increased activity in a given brain area or areas and individual differences in behavior (Madden, Gottlob, et al., 1999; McIntosh et al., 1999). We examined such correlations in this experiment to see if we could find evidence that the functional consequences of activation of various brain regions that support face memory differ with age.

Method

Participants

Twelve young right-handed adults (6 men, 6 women), M = 23.2 years, SD = 2.1, range 20–28 years, and 11 older right-handed adults (6 men, 5 women), M = 70.0 years, SD = 5.7, range 62–79 years, participated in the experiment. All were screened to rule out any diseases or medications that might affect brain function; screening included magnetic resonance imaging (MRI) scans to rule out cerebral or cerebrovascular abnormalities. (One additional older male participant was excluded because of white matter changes on his MRI.) The two groups had equivalent years of education: young, M = 17 years, SD = 1.4; old, M = 15.7 years, SD = 3.3. Scores on the Mill-Hill vocabulary test (Raven, 1982) were lower for the young adults, M = 18.2, SD = 4.8, than were those for the old adults, M = 24.2, SD = 5.5, t(21) = 2.8, p < .05. In addition, the younger adults had slightly higher mental status scores (Folstein, Folstein, & McHugh, 1975), M = 29.5, SD = 0.5, than did the old adults, M = 28.7, SD = 0.8, t(21) =-2.8, p < .05, although all participants scored in the normal range. Participants who needed correctional lenses to view the stimuli wore their own glasses during the experiment. Additional participants, comparable to the positive emission tomography (PET) group in age and years of education (10 young and 12 older adults), were given the face memory tests but were not scanned. There were no differences on the behavioral measures between this group and the PET group, so the data from the two groups were combined to provide more stable measures of accuracy and reaction time. The behavioral results from the PET groups and from the larger groups are both reported. This experiment was approved by the Ethics Committee of Baycrest Centre for Geriatric Care and conducted with the written consent of each participant.

Stimulus Material and Tasks

The face stimuli used in the experiment were black-and-white pictures of faces of young individuals with the clothes and hair cropped from the photo (Haxby et al., 1996). There were three encoding tasks, requiring three lists of stimuli. In each of the three lists, one half of the faces were of men and one half were of women, one half were oriented to the right and one half to the left, and one half had been previously judged to be pleasant or unpleasant in a pilot study. For two of the encoding conditions, participants were instructed to make certain decisions about the stimuli, but were not

explicitly asked to remember them. One of these conditions, the "shallow" condition, required a decision about whether the face was oriented to the participant's right or the left, and the other incidental condition, the "deep" condition, required a decision as to whether the person who was depicted appeared to be pleasant or unpleasant. During the third encoding condition, subjects were instructed to memorize the faces and were told that they would be tested on these items (intentional learning). Following the study conditions, there were three recognition tests to assess memory for faces that were encoded using the three encoding tasks separately. During each encoding task, participants observed 24 unfamiliar faces, and during each recognition task, they observed 32 faces, 16 that had been presented in one of the encoding conditions ("old" faces), and 16 that had not been previously presented ("new" faces). During the recognition tests, participants indicated whether each face was "old" or "new." For all encoding and recognition tasks, stimuli were presented for 2 s each, with a 2-s interval between stimuli. Control stimuli were pictures of distorted faces that resembled abstract designs but were not recognizable as faces. During the control task, participants viewed the stimuli but did not have to perform a specific task. During all tasks, participants pressed one of two mouse buttons, using their right hands, with either their index finger (left mouse button) or middle finger (right mouse button). For the pleasantness judgment and right-left orientation conditions, these button presses indicated the participant's decision about each stimulus (index finger = pleasant or left orientation; middle finger = unpleasant or right orientation). For the intentional learning and control tasks, there was no decision to be made, but button presses with the index finger were required to control for brain activity related to the motor response. For the recognition tasks, participants pressed the button with their index finger to indicate an "old" face and pressed the button with their middle finger to indicate a "new" face.

Scanning Procedure

Eight PET scans, with injections of 40 mCi of H215O each and separated by 11 min, were performed on all participants. Scans 1 and 8 consisted of presentations of the control task, scans 2-4 were encoding tasks, and scans 5-7 were recognition tasks. Scans were performed on a GEMS PC2048-15B tomograph, which has a reconstructed resolution of 6.5 mm in both transverse and axial planes. This tomograph permits 15 planes to be acquired simultaneously, each separated by 6.5 mm (center to center). Emission data were corrected for attenuation by means of a transmission scan obtained at the same levels as the emission scans. Head movement during the scans was minimized with a thermoplastic mask that was molded to each person's head and attached to the scanner bed. Prior to each scan, the instructions for the task to be carried out during that scan were read to the participant. Then the task was begun, and 20 s later the isotope was injected. Each task continued throughout the 1-min scanning period. For the encoding scans, the order of conditions was counterbalanced across participants using a Latin Square design. The three lists of faces were assigned to the three conditions such that each list was encoded using each of the tasks equally often (i.e., one third of the participants encoded the first list using the orientation task, one third used the pleasantness judgment, and one third used the intentional instructions, etc.). The three recognition scans were presented in the same order as were the encoding scans. That is, if the encoding conditions were presented in the order of shallow, then learn, followed by deep, the recognition scans also were presented in this order. Estimates of regional cerebral blood flow (rCBF) were obtained from the measured radioactivity counts in each scan (Herscovitch, Markham, & Raichle, 1983).

Data Analysis

Accuracy of performance during the recognition tests (proportion hits minus proportion false alarms) and mean reaction times for correct responses (in milliseconds) were analyzed using repeated-measures analyses of variance (ANOVA) with encoding task as the repeated measure and group as the independent factor.

Each participant's PET scans were registered to the first scan to correct for small movements during the scanning session using automated image registration (AIR; Woods, Cherry, & Mazziotta, 1992). Images were then spatially normalized to the Talairach and Tournoux atlas coordinate system (Talairach & Tournoux, 1988) and smoothed using a 10-mm filter (to increase signal to noise and to reduce the effects of individual differences in anatomy) by using SPM95 (Frackowiak & Friston, 1994). Ratios of regional cerebral blood flow (rCBF) to global CBF within each scan for each subject were computed and analyzed using Partial Least Squares (PLS). (For a more complete description of this technique, see McIntosh, Bookstein, Haxby, & Grady, 1996.) PLS is a multivariate analysis that identifies groups of brain regions that are distributed over the entire brain that together covary with some aspect of the experimental design, in contrast to the more typically used univariate analysis that assesses the significance of each region separately. The use of this method is based on the assumption that cognition is the result of the integrated activity of dynamic brain networks rather than the action of any one region acting independently. PLS operates on the covariance between brain voxels and the experimental design to identify a new set of variables (so-called latent variables [LVs]). Each LV identifies both the pattern of task differences across the experimental conditions and the brain voxels showing that pattern. Each brain voxel has a weight on each LV, known as a salience, which indicates how that voxel is related to the LV. A salience can be positive or negative, depending on whether the voxel shows a positive or negative relation with the pattern identified by the LV. Multiplying the rCBF value in each brain voxel for each subject by the salience for that voxel and summing across all voxels gives a latent variable score (called a "brain" score here) for each subject for each task condition on a given LV. These scores can be used to examine differences in brain activity across conditions, as greater activity in brain areas with positive (or negative) weights on a latent variable will yield positive (or negative) mean scores for a given condition. In addition, the scores indicate the degree to which each individual expresses a given pattern within a condition.

We carried out PLS analyses on young and old adults separately as well as an analysis of the two groups combined. The specific contrasts compared the encoding and recognition tasks with the average of the two control task runs and to one another. Prior to the group analysis, we removed the effects of any global rCBF differences between the young and old groups by regressing out the group main effect from each voxel for each subject, leaving only the residual variance that resulted from the tasks. The significance of the LVs was assessed using a permutation test (Edgington, 1980; McIntosh et al., 1996), using $p \leq .01$. In addition to the permutation test, we determined the reliability of the saliences for the brain voxels that characterized each pattern. To do this, all saliences in each analysis were submitted to a bootstrap estimation of the standard errors (Efron & Tibshirani, 1986; Sampson, Streissguth, Barr, & Bookstein, 1989). A reliable contribution was made by voxels whose weight on a given LV pattern was greater than twice the estimated standard error of that weight, which corresponds to 95% confidence limits (Sampson et al., 1989). Local maxima for the reliable brain areas on each LV were defined as the voxel with a ratio higher than any other voxel in a 2-cm cube centered on that voxel. Locations of these maxima are reported in terms of brain region, or gyrus, and estimated Brodmann area (BA) as defined in the Talairach and Tournoux atlas.

The correlations between the LVs obtained from the combined-group analysis and those from the two within-group analyses were calculated to obtain an indication of whether one group contributed primarily to a specific combined-group pattern or if both groups contributed equally. Group by task interactions on the LVs from the combined-group analyses were examined by contrasting the corresponding within-group brain scores using an ANOVA. The separately determined scores were compared rather than the scores from the combined analyses because entering group into the design matrix as a variable biases these latter scores. A value of $p \leq .01$ was used for interaction effects. Also, it is important to note that because the ANOVAs were carried out on the brain scores, which reflect activity

across the whole image, any between-group differences apply to the entire pattern of activity and not just to any single region.

PLS also was used to examine the relation between activity in all brain voxels during the encoding and recognition tasks and recognition accuracy (hits-false alarms) in young and old adults. This type of analysis is similar to the task analysis previously described except that it calculates the covariance between brain activity and the behavioral measure rather than the covariance between task contrasts and brain voxels. With this type of analysis, correlations between behavior and brain activity are computed within each condition and then compared across conditions. This allows the identification of regions that are similarly correlated with behavior as well as those areas that are differentially correlated across the different task conditions or between groups (Grady, McIntosh, Bookstein et al., 1998; Schreurs et al., 1997). As with the task PLS analysis, the threshold p value for the LVs was set at $\leq .01$.

Results

Memory Performance

For those individuals participating in the PET experiment, there was no difference between young and old in the number of correct right-left orientation decisions during shallow encoding, young M = 22.1, SD = 2.2; old M = 22.5, SD = 2.5, t(21) = -0.5, or in the number of pleasant decisions in the deep encoding condition, young M = 13.8, SD = 3.3; old M = 15.1, SD = 3.3, t(21) =-0.9. Performance measures on the face recognition tasks in young and old adults are presented in Table 1. Young and old adults showed equivalent proportions of hits in both the PET and combined groups, F's < 1, but the older adults showed more false alarms in both the PET group, F(1, 21) = 11.7, p < .005, and the larger group of participants, F(1, 43) = 21.5, p < .005. The main effect of encoding task on hits minus false alarms in the PET group was significant, F(2, 42) = 3.4, p < .05, as was the main effect of age, F(1, 21) = 9.0, p < .01. The task by age interaction was not significant (F < 1), indicating that older adults showed the same degree of reduced recognition accuracy compared with young adults across all conditions. Post hoc contrasts revealed that the proportion of hits minus false alarms was greater when faces had been encoded using the pleasant-unpleasant judgment compared with the other two tasks, F(1, 21) = 7.2, p < .025. Recognition of faces that were encoded using the shallow task and recognition of faces that were memorized were not significantly different from one another (F < 1). The results were the same for the larger group of participants, that is, the effects of encoding task, F(2, 82) = 8.3, p < .01, and age, F(1, 41) = 21.9, p < .001, were significant but the interaction was not (F < 1). In addition, for the larger groups, the effect of encoding task was significant for the young adults when analyzed separately, F(2, 44) = 4.6, p < .05, and for the older adults, F(2, 44) = 4.0, p < .05. The only significant effect on reaction time was that of age, for both the PET group, F(1,20) = 4.9, p < .05 (1 older adult did not have reaction times because of technical problems), and the combined group, F(1,42) = 16.9, p < .001. However, all older participants had mean RTs of less than 2 s, indicating that they were able to respond with no difficulty within the time frame imposed by the experiment.

Brain Activity: Task Effects

A summary of the statistical results from the three analyses of task effects on brain activity is shown in Table 2. A single significant brain pattern was identified in the combined group

Table 1 Performance on Face Recognition Tasks

	Young	(PET)	Old (I	PET)	You	ng ^a	Old	l ^b
Task	М	SD	М	SD	М	SD	М	SD
			Propo	ortion of hits	5			
Orientation	0.56	0.18	0.63	0.18	0.57	0.16	0.62	0.17
Learn	0.60	0.15	0.69	0.19	0.63	0.17	0.67	0.17
Pleasantness	0.70	0.14	0.69	0.15	0.70	0.15	0.68	0.15
			Proportion	n of false al	arms			
Orientation	0.31	0.15	0.48	0.18	0.34	0.16	0.52	0.16
Learn	0.32	0.16	0.53	0.18	0.34	0.16	0.52	0.15
Pleasantness	0.30	0.11	0.45	0.17	0.29	0.12	0.46	0.17
			Hits-	false alarms	5			
Orientation	0.25	0.16	0.15	0.18	0.24	0.18	0.10	0.19
Learn	0.29	0.20	0.15	0.15	0.29	0.17	0.15	0.14
Pleasantness	0.40	0.16	0.24	0.15	0.41	0.20	0.22	0.15
			Reacti	on time (m	5)			
Orientation	1,206	204	1,403	234	1,189	178	1,417	206
Learn	1,209	212	1,426	251	1,191	186	1,391	184
Pleasantness	1,212	188	1,402	275	1,180	173	1,401	198

Note. Young (PET) and Old (PET) refer to groups participating in the imaging study (N = 12 and N = 11, respectively). PET = positron emission tomography. ^a Young N = 22. ^b Old N = 23.

		LV significan	ice	LV corre	elations ^a
Analysis	Young	Old	Combined	Young	Old
Encoding vs. control LV1	<.001	<.01	<.001	.99	.97
Recognition vs. control LV1	<.001	<.001	<.001	.99	.71
Recognition vs. control LV2	ns	ns	<.001	.60	89
Encoding vs. recognition LV1	<.001	<.001	<.001	.84	.79
Encoding vs. recognition LV2	ns	ns	<.001	.40	46

 Table 2

 Results of the Partial Least Squares Task Analyses

Note. LV = latent variables.

^a Correlations between within-group LVs and LVs from the combined analysis.

analysis of the face encoding conditions to the control task, which was contributed to by both young and old adults (as indicated by the large correlations between the within-group LVs and combined LV seen in Table 2). The group by task interaction also was significant, F(3, 63) = 5.2, p < .01. This interaction was attributed to the fact that young adults showed a difference in brain activity between the pleasantness judgment and all other tasks, whereas in older adults, the control task and shallow encoding task were distinguished from the deep encoding and learning conditions, post hoc F(1, 21) = 11.5, p < .01 (Figure 1). Areas with increased activity during the pleasant-unpleasant discrimination in both groups included inferior prefrontal regions and the left amygdala (Figure 1 and Table 3). In older adults, increased activity in these regions also was seen during intentional learning. Areas with increased activity during the control task in young adults, and in the control task and right-left judgment in older adults, were found mainly in temporal regions. Despite the fact that both old and young adults contributed to this encoding pattern, the overall contribution of the young adults appeared to be stronger (note the regions that were not reliably activated in the older adults, see Table 3).

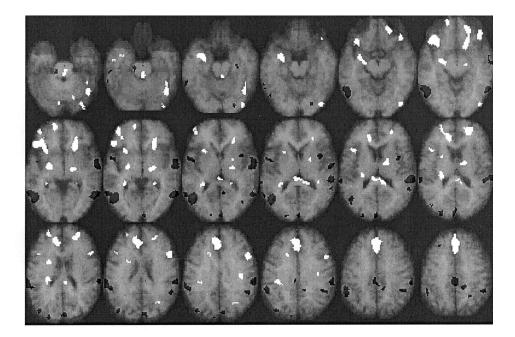
The comparison of the face recognition and control conditions resulted in two significant LVs in the combined analysis (Table 2). The first LV correlated positively with the LVs from the young and old adults; however, there was a significant task \times group interaction on the scores, F(3, 63) = 15.1, p < .001. This interaction was a result of a difference in the relation of brain activity during the recognition of shallowly encoded faces to activity in the other two recognition conditions (Figure 2); that is, the areas identified by this LV differentiated all recognition conditions from the control task in young adults, but distinguished only the learn and deep conditions from the control task in older adults (similar to the effect seen during encoding; compare the brain scores for older adults in Figures 1 and 2). Increased activity during recognition was seen in bilateral prefrontal cortex, left premotor cortex, and in a few posterior regions, including the cingulate gyrus (positive saliences on LV1, Table 4). Greater activity during the control task in young adults and in the control and shallow conditions in older adults was found mainly in posterior regions, including extrastriate and temporal cortices (negative saliences on LV1, Table 4). The second combined LV also was correlated with both of the within-group LVs, but was positively correlated with the LV in the younger adults and negatively correlated with the LV in older adults (Table 2). This pattern thus identified regions with opposite patterns of activity in young and old adults during recognition. This effect was most prominently seen in a left anterior temporal region and one in premotor cortex, where only the older adults had increased activity during recognition (Table 4, positive salience on LV2), and an area in right dorsolateral prefrontal cortex, where only the young adults had increased activity during recognition (Table 4, negative salience on LV2).

In the comparison of the encoding and recognition conditions, the first significant combined-group pattern was contributed to equally by young and old adults (Table 2), but there was a significant three-way interaction of memory task by encoding task by group, F(2, 42) = 8.2, p < .01. This interaction effect confirmed the differences seen in the separate analyses of encoding and recognition and resulted from a reduction in brain activity during the shallow conditions in the older adults, whereas there was no systematic variation resulting from encoding task in the young adults (Figure 3). The brain areas with increased activity during face encoding, compared with recognition, were mainly in ventral occipital and temporal cortices bilaterally, including the right hippocampal region (Table 5). Conversely, the areas with increased activity during face recognition, compared with encoding, were mainly in bilateral prefrontal cortex and occipitoparietal regions. In addition, it is clear that the increases in left temporal regions during encoding (e.g., BAs 37 and 38 in Table 5) were attributed mainly to the young adults, and the increase in left anterior prefrontal cortex during recognition (BA 10 in Table 5) was attributed mainly to the contribution of the older adults.

The second combined pattern in the comparison of encoding to recognition also characterized both young and old adults (Table 2), although the correlations were in opposite directions, indicating opposite effects during the tasks; that is, there were several areas where young adults had more activity during encoding than during recognition and where the old adults had the opposite pattern (Figure 4A). These areas were in left prefrontal cortex (BA 45, X:-42, Y:24, Z:0) and the anterior cingulate (BA 32, X:4, Y:40, Z:16). This difference in activity during memory tasks in young and old adults is shown for the left prefrontal region in Figure 4B.

Brain-Behavior Correlations

The analysis of the correlations between brain activity and recognition accuracy identified two significant LVs, one in which young and old adults had different patterns of correlation across the tasks and one in which the pattern of correlation was the same. The first LV (p < .001, Figure 5) identified regions that were differently correlated in the two groups. A group of mostly limbic



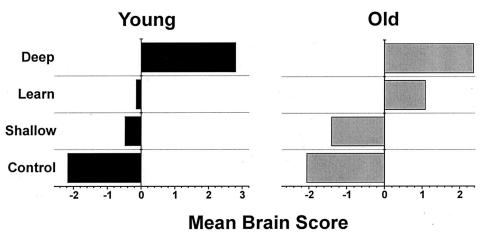


Figure 1. At the top of the figure, the brain areas with differential activity during the encoding and control tasks are shown on a standard MRI for young and old adults (brain areas from the combined-group analysis with a reliability ratio ≥ 2.0). Unless otherwise noted, in this and subsequent figures, the brain slices begin at -28 mm relative to the anterior commissure-posterior commissure line (AC-PC line; top left image) and end at +40 mm (bottom right image) with a 4-mm slice separation. The graphs at the bottom of the figure show the mean brain scores for young and old adults on the LVs from the within-group analyses that correlated with this combined LV. Positive mean brain scores were found in those conditions where activity was increased in the brain regions shown in white (i.e., those with positive salience on the LV). Negative mean brain scores were found in those conditions where activity was increased in the brain regions shown in black (i.e., those with negative salience on the LV). See Table 3 for local maxima of these regions.

regions showed an association between increased activity and better recognition of faces in young adults. These areas included the hippocampus bilaterally, orbitofrontal cortex, and the left temporal pole (Table 6, positive saliences on LV1). A different set of regions, including bilateral posterior temporal and occipital regions and right prefrontal cortex showed positive correlations between activity and recognition of faces in older adults across all three conditions (Figure 5 and Table 6, negative saliences on LV1). These patterns of correlation in both groups were similar for the encoding and recognition conditions, and thus represent memory-related correlations that are not specific to either encoding or recognition.

The second LV (p < .001) identified a set of brain regions where activity was similarly correlated with memory performance in both young and old adults (Figure 5). Better recognition of faces encoded using the pleasantness judgment was correlated with increased activity in three left hemisphere regions, two in prefrontal cortex and one in posterior temporal cortex (Table 6, positive

Region, gyrus	Hemisphere	Brodmann area	X	Y	Ζ	Young ^a	Old ^b
		Positive sali	ences ^c				
Prefrontal							
GFi	R	47	38	28	-12	2.47	1.73
GFi	L	47	-36	26	-8	2.22	1.84
GFd	L	10	-16	54	$^{-4}$	3.22	1.24
GFm	R	10	22	48	16	3.17	0.74
GFm	L	10	-42	50	0	3.13	1.72
Cingulate	L	32	-8	28	28	2.90	1.85
Amygdala	L	_	-30	-4	-16	3.45	2.22
Temporal (GTs)	L	42	-24	-30	16	2.85	2.04
Occipital (GF)	R	37	40	-60	-24	2.24	2.41
		Negative sal	iences ^d				
Temporal							
GTi	R	37	52	-60	-4	-3.25	-1.00
GTi	L	37	-44	-68	4	-4.25	-2.63
GTs	R	22	54	-10	0	-2.63	-2.15
GTs	R	22	54	-32	12	-2.89	-2.93
Cingulate	Μ	31	-2	-34	40	-3.62	-1.63

Brain Areas Identified by the Contrast of the Face Encoding Tasks and the Control Task in Young and Old Adults

Note. Coordinates and estimated Brodmann areas of all maxima (Talairach & Tournoux, 1988) are from the combined group analysis (areas at least 30 voxels in size). X (right–left): Negative values are in the left hemisphere; 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. R = right; L = left; M = midline (≤ 5 mm from zero point in X dimension); GF = fusiform gyrus; GF(m,i,d) = frontal gyrus (middle, inferior, medial); GT(s,i) = temporal gyrus (superior, inferior). ^a Salience/s.e. ratio from the within-group analysis of the young adults. ^b Salience/s.e. ratio from the gyrus (superior).

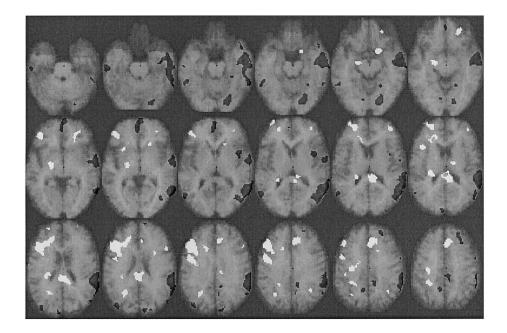
saliences on LV2). Alternatively, better recognition of faces that had been shallowly encoded or intentionally learned was associated with increased activity mainly in extrastriate visual areas (Table 6, negative saliences on LV2).

Table 3

Discussion

The behavioral results from this experiment are consistent with those of previous studies in terms of both the effects of encoding task and the effect of aging on face recognition (Smith & Winograd, 1978). Young and old adults both showed a benefit of the deep encoding task, in this case a pleasant/unpleasant judgment, on later recognition performance. However, the intentional learning task resulted in recognition performance that was no different from that seen after purely perceptual or shallow encoding, which is consistent with other reports on face memory (Smith & Winograd, 1978). This finding is in contrast to previous studies of the effect of encoding task on recognition of pictures of objects and words (Grady et al., 1999; Grady, McIntosh, Rajah, & Craik, 1998). In those experiments, recognition of pictures and words increased after both deep processing and intentional learning compared with shallow processing in young and old adults. This difference of type of stimulus may indicate that unfamiliar faces are more difficult to intentionally learn and remember, perhaps because they lack the kind of readily accessible semantic information contained in both words and pictures of objects. In addition, these results illustrate the power of making an emotionally based judgment on aiding memory for faces, which could reflect the general beneficial effect of emotional processing on memory (e.g., Adolphs, Cahill, Schul, & Babinsky, 1997). However, regardless of encoding task, the older adults showed reduced face recognition, indicating the robust nature of age-related differences in face memory. This reduction was accounted for mainly by the increase in false alarm rate in the older adults, similar to that reported for face recognition by a number of investigators (e.g. Bartlett et al., 1989; Crook & Larrabee, 1992; Smith & Winograd, 1978). Given that there were no differences in task performance during encoding or any significant interactions of encoding task and age on recognition scores, the greater difficulty in remembering the faces shown by older adults is reflected equally across the tasks. It is therefore unlikely that the specific task demands affected the two age groups differently.

A summary of the imaging results is shown in Table 7. We will discuss these results first in relation to the previous work on face processing in the older adults, then address the question of how encoding task affected brain activity. Finally, we will consider the brain areas where older adults had greater activity or which were differentially related to behavior and how these results influence the idea of compensatory changes in elderly people. The current experiment replicated several aspects of the previous study of face memory (Grady et al., 1995), including the finding that there was generally less activity in left frontotemporal regions during encoding in older adults. This relative reduction in left hemisphere activation during encoding in older adults also has been seen in previous reports of verbal memory (Anderson & Grady, 2001; Cabeza et al., 1997). The similar findings for verbal and nonverbal



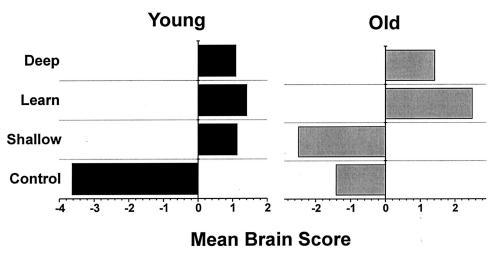


Figure 2. The brain areas with differential activity in the comparison of the recognition and control tasks are shown on a standard MRI for young and old adults (brain areas from the combined-group analysis with a reliability ratio ≥ 2.0). The graphs at the bottom of the figure show the mean brain scores for young and old adults on the LVs from the within-group analyses that correlated with this combined LV. Positive mean brain scores indicate that activity in those tasks was increased in the brain regions shown in white (i.e., those with positive salience on the LV). Negative mean brain scores indicate that activity was increased in the brain regions shown in black (i.e., those with negative salience on the LV). See Table 4 for local maxima of these regions.

stimuli suggest that reduced activity in these regions during encoding in older adults is not specific to stimulus type but may reflect a general encoding deficit. On the other hand, we found here, as was reported earlier, that older and younger adults had equivalent degrees of right prefrontal activity during face recognition, at least when recognition and encoding were compared directly. In particular, a region in right anterior prefrontal cortex (right BA 10 in Table 5) was found to be active during recognition in both young and old groups. This region is almost ubiquitously found to be activated during memory retrieval, regardless of how retrieval is assessed (for reviews, see Grady, 1999; Lepage, Ghaffar, Nyberg, & Tulving, 2000), although its precise role in retrieval is still under some dispute (Buckner, Koutstaal, Schacter, Wagner, & Rosen, 1998; Henson, Shallice, & Dolan, 1999; Lepage et al., 2000; Rugg, Fletcher, Frith, Frackowiak, & Dolan, 1996; Wagner, Desmond, Glover, & Gabrieli, 1998). Also similar in degree of activation between age groups was the right fusiform gyrus, which was active during the pleasantness judgment condition compared with the control task. This finding is consistent with previous reports of a lack of an age-related reduction in this region during face perception and short-term memory tasks (Grady et al., 1994; Grady, McIntosh, Bookstein, et al., 1998). One notable difference

Region, gyrus	Hemisphere	Brodmann area	X	Y	Ζ	Young ^a	Old ^b
		LV1: positive	saliences				
Prefrontal							
GOb	R	11	20	38	-8	2.89	1.23
GFm	L	46	-44	40	0	3.09	2.88
GFm	L	9	-42	24	28	2.89	1.55
GFm	L	10	-24	50	16	2.10	2.00
Premotor (GPrC)	L	6	-44	-2	28	2.48	2.90
Cingulate	R	30	6	-42	16	2.83	3.08
	М	32	0	22	40	1.72	2.31
Temporal (GTm)	L	39	-24	-58	24	1.99	2.02
		LV1: negative	saliences				
Prefrontal (GFs)	R	8	20	38	40	-2.79	-1.78
Cingulate	L	32	-6	48	4	-2.42	-3.04
6	R	23	8	-46	32	-2.76	-1.59
Temporal							
GTi	R	20	52	-42	-24	-2.21	-2.15
GTm	R	21	52	-2	-16	-3.35	-1.48
GTm	R	21	58	-58	0	-3.80	-0.87
GTm	L	37	-54	-66	8	-3.00	-0.98
GTs	R	22	54	-42	20	-3.08	-2.01
GTs	R	22	54	-8	4	-2.36	-1.83
Occipital							
GĹ	R	18	14	-80	-16	-2.27	-3.15
GOm	L	19	-38	-82	24	-2.53	-1.69
Parietal (LPi)	R	40	56	-38	36	-2.11	-1.22
		LV2: positive	saliences				
Prefrontal (GFd)	L	9	-6	50	20	-1.93	0.79
Premotor (GPrC)	L	6	-48	4	12	-0.34	2.58
Temporal (GTs)	L	38	-42	12	-12	-0.67	2.84
Extrastriate (GL)	М	18	-2	-62	4	-1.04	1.13
Midbrain	L		-16	-20	-20	-1.14	1.73
		LV2: negative	saliences				
Prefrontal							
GFd	L	10	-14	50	-4	1.16	-1.89
GFm	R	46	36	30	32	2.61	-1.99

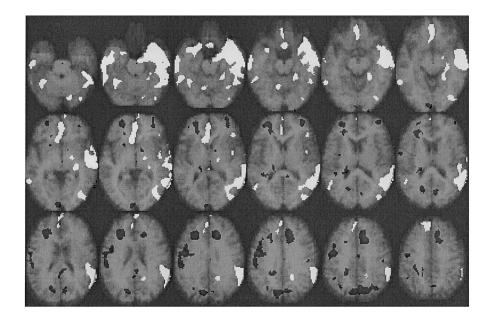
Brain Areas Identified by the Contrast of the Face Recognition Tasks and the Control Task in Young and Old Adults

Note. Coordinates and estimated Brodmann areas of all maxima (Talairach & Tournoux, 1988) are from the combined group analysis (areas at least 30 voxels in size). X (right–left): Negative values are in the left hemisphere; 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. R = right; L = left; M = midline (≤ 5 mm from zero point in X dimension); GL = lingual gyrus; GOm = middle occipital gyrus; GF(s,m,d) = frontal gyrus (superior, middle, medial); GOb = orbitofrontal gyrus; GPrC = precentral gyrus; GT(s,m,i) = temporal gyrus (superior, middle, inferior); LPi = inferior parietal. ^a Salience/s.e. ratio from the within-group analysis of the young adults. ^b Salience/s.e. ratio from the within-group analysis of the young adults.

between the results of this experiment and the previous study of episodic face memory (Grady et al., 1995) was that older adults showed reliable activation of the right hippocampal region during encoding only in the current experiment. Although this suggests that medial temporal regions can be activated during face encoding in older adults under some conditions, the differential correlations noted between hippocampal activity and accuracy of face recognition in younger and older adults (discussed in more detail below) provides further evidence that function of this region is altered in older adults during face memory.

Table 4

As one would expect, both young and older adults showed an effect of encoding task on brain activity during encoding (see Table 7). During encoding, the main effect of encoding task on brain activity in both young and old adults distinguished the deep encoding condition primarily from the nonface control condition (as we have reported previously for the young adults, Bernstein, Beig, Siegenthaler, & Grady, 2002). The brain areas that mediate the judgment of a face's pleasantness in both groups included ventral frontal and occipitotemporal regions and the amygdala. These areas have previously been shown to have increased activity



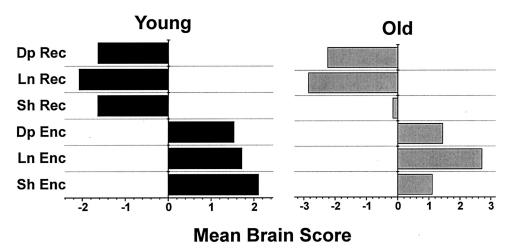


Figure 3. The brain areas that showed differential activity in the comparison of the recognition and encoding tasks are shown on a standard MRI for young and old adults (brain areas from the combined-group analysis with a reliability ratio ≥ 2.0). The graphs at the bottom of the figure show the mean brain scores for young and old adults on their respective LVs. Positive mean brain scores indicate that activity in those tasks was increased in the brain regions shown in white (i.e., those with positive salience on the LV). Negative mean brain scores indicate that activity was increased in the brain regions shown in black (i.e., those with negative salience on the LV). See Table 5 for local maxima of these regions.

during face encoding (Haxby et al., 1996; Kelley et al., 1998) or processing of the emotional content of faces (Morris et al., 1998; Whalen et al., 1998), suggesting an interaction of visual and emotional processing in making the pleasant-unpleasant judgment. In addition, both young and old adults showed brain activity that characterized face recognition, compared with the control task, consisting of increased activity in frontal, posterior cingulate, and temporoparietal regions. This pattern of activity is consistent with retrieval patterns reported for a variety of stimuli (for a review, see Cabeza & Nyberg, 2000). However, even though both young and old adults showed these brain activity patterns that are characteristic of memory, there were age-related differences during both encoding and recognition in the way that these patterns of activity was expressed across the tasks. That is, in younger adults, the pleasantness task alone resulted in activation of the ventral frontal regions and amygdala, whereas in older adults the intentional learning task also was accompanied by increases in these regions. During recognition, the young adults showed no differences across tasks based on how the faces were initially encoded, but the older adults showed the recognition pattern only when attempting to recognize the faces that were encoded with either the pleasantness or intentional task. Thus, across all task contrasts (i.e., in Figures 1–3), it is clear that for older adults, the pleasantness and intentional tasks were accompanied by similar brain activity patterns

Region, gyrus	Hemisphere	Brodmann area	X	Y	Ζ	Young ^a	Old ^b
		Encoding > red	cognition				
Prefrontal (GFs)	L	8	-10	40	44	2.41	2.16
Cingulate	М	24	-4	30	4	3.98	1.78
Temporal							
GŤi	L	37	-58	-50	-8	4.96	1.75
GTi	L	20	-46	-14	-24	5.03	1.31
GTm	R	21	56	-52	8	5.10	2.07
GTs	R	38	34	14	-20	2.32	2.93
GTs	L	38	-32	4	-20	3.16	1.68
Amygdala	R	_	18	-4	-20	0.54	2.97
Hippocampus/GH	R	_	24	-28	-4	1.64	2.55
** *	R	35	18	-40	-12	2.65	1.78
Parietal (LPi)	R	40	54	-44	28	2.68	2.70
Occipital (GOm)	R	19	36	-82	8	2.72	2.01
Caudate nucleus	L		-8	22	0	2.87	2.90
		Recognition E	ncoding				
Prefrontal (GFm)	R	10	32	50	8	-2.14	-2.40
	L	10	-26	48	0	-1.15	-2.80
	L	46	-28	28	24	-2.62	-2.59
Premotor (GPrC)	L	6	-44	-4	32	-2.24	-1.88
Cingulate	R	24/32	14	14	36	-1.62	-2.44
Parietal							
LPi	L	40	-52	-26	28	-1.89	-2.48
Pcu	L	31/7	-24	-42	32	-1.11	-2.48
LPs	R	7	32	-70	36	-3.14	-1.16
Occipital (Cu)	L	19	-10	-76	32	-3.00	-1.98

Local Maxima of Areas With Activity Differentiating Encoding and Recognition of Faces in Young and Old Adults

Note. Coordinates and estimated Brodmann areas of all maxima (Talairach & Tournoux, 1988) are from the combined group analysis (areas at least 30 voxels in size). X (right–left): Negative values are in the Left Hemisphere; 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. R = right; L = left; M = midline (≤ 5 mm from zero point in X dimension); Cu = cuneus; GH = parahippocampal gyrus; GOm = middle occipital gyrus; GF(s,m) = frontal gyrus (superior, middle); GPrC = precentral gyrus; GT(s,m,i) = temporal gyrus (superior, middle, inferior); LPi = inferior parietal; LPs = superior parietal; Pcu = precuneus.

^a Salience/s.e. ratio from the within-group analysis of the young adults. ^b Salience/s.e. ratio from the withingroup analysis of the old adults.

(which were in turn similar to those seen in young adults), whereas the perceptual conditions showed brain activity that was similar to that seen during the nonface control task. In other words, the older adults showed reductions in brain areas that are important for memory when the encoding task emphasized shallow processing of the faces. This is consistent with our hypothesis that more effective encoding tasks would result in fewer age-related reductions in brain activity. Curiously, the brain results in the older adults were not completely consistent with the behavioral results, because memory performance was not improved after memorization, unlike the improvement seen after the pleasantness judgment, despite the similarity of brain activity in the two conditions. However, this differentiation of brain activity during shallow processing from that seen during deeper processing is strikingly similar to that found during encoding of pictures of objects (Grady et al., 1999). In that earlier experiment, both young and older adults had a pattern of activity that differentiated deep encoding and memorization of pictures from shallow picture encoding. These two experiments together provide evidence that encoding

Table 5

tasks that presumably encourage deeper processing can alter the underlying brain activity of older adults, at least for complex visual stimuli, by better engaging the brain systems that underlie these memory processes in young adults. Further, this appears to result in a greater dependence on initial encoding task of brain activity in older adults during face recognition, where young adults show no effect at all.

In addition to these reductions in brain activity in older adults, we found, as others have before us (Anderson & Grady, 2001; Cabeza, Anderson, Houle, Mangels, & Nyberg, 2000; Cabeza et al., 1997; Madden, Turkington, et al., 1999), that young adults had increased activity in a region of left ventral prefrontal cortex during encoding, whereas older adults showed an increase in this area during recognition. Older adults also had reliable bilateral anterior prefrontal activation during recognition (see Tables 5 and 7). Because young adults often have mainly, but not exclusively, right frontal activation during retrieval (for a review, see Nyberg, Cabeza, & Tulving, 1996), this finding suggests that older adults have an alteration in the memory-related specialization of the

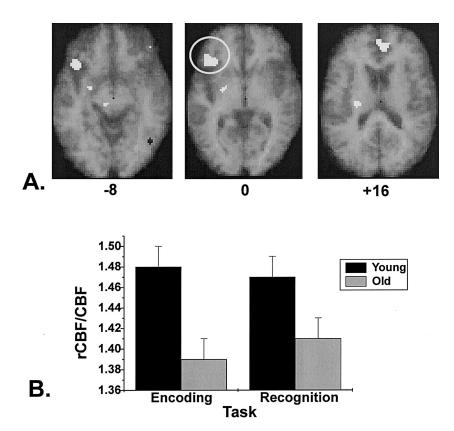


Figure 4. A. The brain areas where young and old adults showed opposite activity related to face encoding and recognition are shown on standard MRIs (LV2 from the combined-group analysis, brain areas with a reliability ratio ≥ 2.0). The numbers below the brain images indicate the Z value relative to the AC-PC line. White areas are those where young adults showed greater activity during encoding and old adults had greater activity during recognition. Only one region had the opposite pattern and is shown in black. B. The scaled rCBF values for young and old adults in the left prefrontal region (circled in the top panel) are shown.

frontal lobes that may not be specific to any one type of information. These additional activations of left prefrontal areas during recognition in older people may reflect a greater need for cognitive resources (Craik & Byrd, 1982) or effortful search during retrieval (Moscovitch, 1992) beyond that necessary for younger adults under most circumstances. Alternatively, this result could reflect an increased demand on semantic retrieval (Cabeza et al., 1997; Kapur et al., 1994), perhaps resulting from the relative lack of activity in this region during encoding. The recruitment of left prefrontal cortex has been interpreted as a compensatory mechanism, particularly when it is associated with performance in older adults that is equivalent to that seen in the young (e.g., Cabeza et al., 1997). Interestingly, activity in this part of left prefrontal cortex was associated with better recognition of deeply encoded faces in both age groups despite different task-related activity in this region in the groups. Therefore, the role of this region in face memory appears not to be compensatory in older adults per se, but rather is related to an improved ability to recognize faces regardless of age.

The third aspect of interest regarding brain activity was the correlation between activity and memory performance (Table 7). Both young and older adults had a brain-behavior correlation pattern that distinguished encoding using the pleasantness judg-

ment and recognition of these faces from the other two conditions. Left prefrontal and temporal activity increased as recognition of faces encoded with the pleasantness task increased. This is consistent with the general semantic nature of activity in these regions (for reviews, see Cabeza et al., 2000; Grady, 1999), even though the "deep" task in this experiment undoubtedly differs from more traditional semantic tasks. Activity in visual areas was associated with recognition of faces that had been encoded using the orientation and intentional learning tasks, both of which could arguably be considered to be more perceptual than the pleasant-unpleasant task. This pattern of brain-behavior correlations was consistent with the behavioral results in both groups, in that the deep condition was dissociated from the other two.

However, this analysis also showed a difference between age groups in the brain areas where activity was correlated with recognition performance. The pattern that accounted for the most covariance in this analysis was one that completely distinguished the two groups in terms of the brain areas where activity was correlated with behavior. In young adults, increased activity in hippocampal and orbitofrontal regions was positively correlated with memory for faces, whereas in older adults, there was a positive association between activity in right prefrontal and parietal regions and memory performance. This finding suggests that

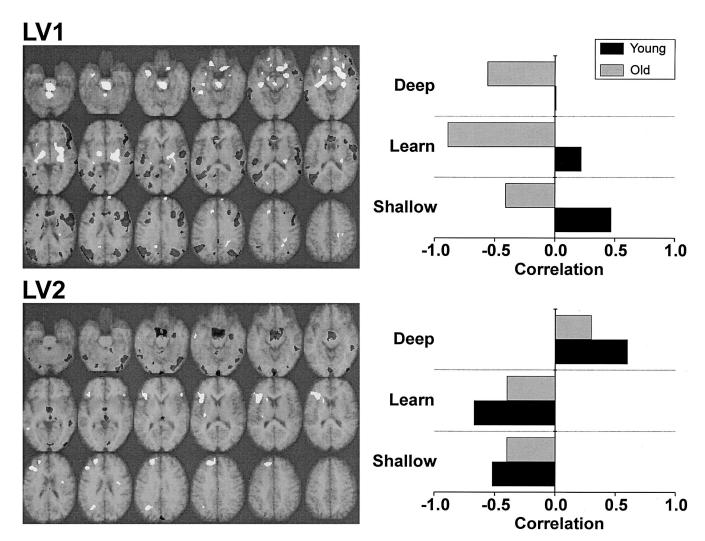


Figure 5. The brain areas that showed correlations between activity and recognition accuracy (hits–false alarms) on LV 1 and LV 2 are shown on a standard MRI for young and old adults combined (brain areas with a reliability ratio ≥ 2.0). The graphs at the right of the figure show the mean correlation values between brain scores and accuracy (averaged across encoding and recognition for each condition) for young and old adults. A positive correlation between brain scores and behavior in a given condition or group indicates that increased activity in the brain regions shown in white (i.e., those with positive salience on the LVs) is associated with increased accuracy. Conversely, negative correlations between brain scores and behavior indicate that increased activity in the brain regions shown in black (i.e., those with negative salience on the LVs) is associated with increased accuracy. See Table 6 for local maxima of these regions.

in young adults, memory for faces is facilitated by activity in medial temporal regions that are known to be critical for memory in general (e.g., Eichenbaum, Otto, & Cohen, 1992; Nadel & Moscovitch, 1997; Squire, 1992). In older adults, activity in medial temporal cortex does not facilitate memory. This is consistent with the previous finding that older adults may not utilize the hippocampus for face memory (Grady, McIntosh, Bookstein, et al., 1998; Grady et al., 1995) and further highlights the importance of this region for age-related memory changes. On the other hand, those areas that show a positive correlation between activity and recognition performance specifically in older adults may be those for which a case for compensation can be made. There are few studies on brain-behavior correlations in older adults, but the

available evidence indicates that these correlations can be quite different in older adults compared with young adults (Grady, McIntosh, Bookstein, et al., 1998; Madden, Gottlob, et al., 1999; McIntosh et al., 1999; Rypma & D'Esposito, 2000) and that prefrontal, superior temporal, and parietal regions are involved in these changes. Even though the specific regions in these parts of cortex may differ across experiments, these reports, along with our data, suggest that prefrontal and temporoparietal regions assume a larger role in the mediation of memory performance with age. In the case of face memory, the "compensatory" regions are not specific to face processing per se, but are part of a more general memory-related set of brain areas. These include dorsolateral prefrontal cortex, thought to mediate maintenance of information

Region, gyrus	Hemisphere	Brodmann area	X	Y	Ζ	Ratio
		LV1: positive salience	es			
Prefrontal (GOb)	R	11	22	22	-12	3.15
Amygdala/putamen	R		24	-4	-8	3.37
Hippocampus	R		24	-22	-4°	2.59
Inppotumpus	L		-26	-20	-8	2.79
Temporal (GTs)	Ĺ	38	-34	-2	-20°	2.91
Midbrain	M	—	-2	-26	-24	3.56
		LV1: negative salienc	es			
Prefrontal						
GFm	R	9	46	22	28	2.84
GFi	R	47	44	34	-4	3.29
Cingulate	L	24	-6	24	16	3.52
Premotor (GPrC)	R	6	42	2	28	3.52
Temporal						
GTm	R	39	30	-72	28	3.16
GTs	R	22	48	-12	4	2.92
GTs	L	42	-46	-26	8	2.88
Extrastriate						
GF	L	37	-34	-56	4	3.63
GOi	L	18	-30	-88	0	2.56
GOm	L	39	-34	-74	24	3.03
		LV2: positive salience	es			
Prefrontal						
GFi	L	45	-36	24	12	2.75
GFm	L	9	-22	46	28	2.53
Temporal (GTm)	L	39	-28	-60	24	2.56
		LV2: negative salienc	es			
Amygdala	R	_	28	-10	-16	2.51
Extrastriate						
GL	R	18	24	-86	-20	2.52
GL	М	18	-2	-100	-16	2.85
GF	R	37	50	-44	-16	2.31
GF	L	37	-50	-60	-24	2.28
Midbrain	R	_	6	-10	-12	2.69
	М	_	2	-26	0	2.50

Local Maxima of Areas Where Activity Is Related to Memory Performance
in Young and Old Adults

Note. Coordinates and estimated Brodmann areas of all maxima (Talairach & Tournoux, 1988) are from the combined group analysis of brain and behavior (areas at least 30 voxels in size). X (right–left): Negative values are in the left hemisphere; 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. R = right; L = left; M = midline (≤ 5 mm from zero point in X dimension); GF = fusiform gyrus; GL = lingual gyrus; GOb = orbitofrontal gyrus; GOi = inferior occipital gyrus; GOm = middle occipital gyrus; GF(m,i) = frontal gyrus (middle, inferior); GPrC = precentral gyrus; GT(s,m) = temporal gyrus (superior, middle).

in working memory (D'Esposito, Postle, Ballard, & Lease, 1999; Petrides, 1994), and temporoparietal cortex, which may play a role in retrieval of information from memory storage (Nyberg et al., 1995; Smith & Jonides, 1997). In addition, the areas where increased activity was correlated with better memory performance indicate a more bilateral pattern in older adults in both anterior and posterior regions of cortex (see Table 7), consistent with greater bilaterality in working memory tasks seen in older adults (Reuter-Lorenz et al., 2000). Thus, with the exception of activity during encoding, older adults often have more bilateral increases of brain activity during memory tasks, indicating that cognitive networks can become more widely distributed with age (see the Cabeza, 2002, article in this volume for a more detailed discussion of this issue).

In conclusion, we have shown that the face recognition performance of young and old participants benefits equally from deeply encoding stimuli compared with shallow encoding of the faces or intentionally trying to memorize them. Older adults did, however, show reduced face memory regardless of encoding task, primarily because of an increased false alarm rate. Both groups showed an effect of encoding task on brain activity during encoding that distinguished the pleasant-unpleasant condition and was consistent

Table 6

Table 7Summary of Imaging Results

Result	Young	Old
Effect of encoding task on brain activity during encoding	+	+
Effect of encoding task on brain activity during recognition	_	+
Encoding related increases in activity		
Left ventral prefrontal	+	_
Right ventral prefrontal	+	+
Left inferior temporal	+	_
Right inferior temporal and fusiform	+	+
Recognition related increases in activity		
Right anterior prefrontal activity	+	+
Left anterior prefrontal activity	_	+
Positive correlations with behavior		
Hippocampus	+	_
Left prefrontal	+	+
Right prefrontal	_	+
Left temporoparietal	+	+
Right temporoparietal	_	+

Note. A plus sign indicates the presence of a reliable effect; a minus sign indicates the absence of a reliable effect.

with the emotional nature of this discrimination. However, only the older adults showed additional changes in brain activity during encoding and recognition that were related to the initial encoding task. These changes were consistent with the idea that providing older adults with more effective ways of encoding will result not only in better memory performance but also in fewer age-related reductions in brain activity. When individual differences in the relation between brain activity and face recognition accuracy were examined, an age difference was noted such that better recognition in young adults was correlated with increased activity in hippocampus and related limbic areas, whereas better recognition in older adults was correlated with increased activity in prefrontal and temporoparietal cortices. These differences suggest agerelated changes in the functional brain organization that underlies face memory that may compensate for reductions in hippocampally mediated memory processing. One question that remains for future research to address is the neural mechanism underlying the increased false alarm rate in the elderly. The newer technique of event-related functional MRI (fMRI) should allow us to separately examine the brain activity for hits and false alarms in young and old adults that perhaps will shed light on this enduring issue in cognitive aging.

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