

# AGE-RELATED CHANGES IN THE NEURAL CORRELATES OF DEGRADED AND NONDEGRADED FACE PROCESSING

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In order to explore the neural correlates of age-related changes in visual perception of faces, positron emission tomographic scans were obtained on young and old adults while they were engaged in tasks of nondegraded and degraded face matching. Old adults were less accurate than were young adults across all face matching conditions, although the age difference was greatly reduced when degraded performance was adjusted for nondegraded performance. The interaction of age and degree of degradation on performance measures was not significant. Brain activity patterns during nondegraded face matching were similar in the two groups with some differences in parietal and prestriate cortices (greater activity in young adults) and in prefrontal cortex, thalamus, and hippocampus (greater activity in old adults). Increases in activity related to increasing degradation of the faces were seen mainly in prefrontal cortices in both age groups. Despite this similarity in the brain response to face degradation, there were striking differences between groups in the correlations between brain activity and degraded task performance. Different regions of extrastriate cortex were positively correlated with behavioural measures in the two groups (fusiform gyrus in the young adults and posterior occipital regions in old adults). In addition two areas where older adults showed greater activity during nondegraded face matching, thalamus and hippocampus, also showed positive correlations with behaviour during the degraded tasks in this group, but not in the young group. Thus, although the elderly are not more vulnerable to the effects of increasing face degradation, the brain systems involved in carrying out these visual discriminations in young and old adults are not the same. These results are consistent with the idea of functional plasticity in face processing over the life span.

## INTRODUCTION

Older individuals have changes in the visual system that affect contrast sensitivity and other aspects of vision (e.g. Spear, 1993). These changes, most of which are thought to be of central rather than

peripheral origin (Burton, Owsley, & Sloane, 1993; Spear, Moore, Kim, Xue, & Tumosa, 1994), affect older adults' ability to detect or discriminate faces, as indexed by an increase in contrast necessary for discrimination to take place in elderly subjects (Owsley, Sekuler, & Boldt, 1981; Sekuler &

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Owsley, 1982). The reduced ability of the elderly to simply discriminate faces is smaller in magnitude than the age-related difference found in the ability to remember faces (Bartlett & Leslie, 1986; Bartlett, Leslie, Tubbs, & Fulton, 1989; Grady et al., 1995) but perceptual changes could have an adverse effect on memory for visual stimuli of all types, including faces. The purpose of the current experiment was to examine performance and brain activity in older adults during degraded face perception tasks under the assumption that understanding of higher-order processes such as face memory will not be complete unless we also understand age-related changes in lower-level perceptual function.

Perception of visual stimuli, including faces, declines as they are degraded or blurred (e.g. Frazier & Hoyer, 1992; Harmon, 1973; Harmon & Julesz, 1973; Hellige, 1976). The effect of ageing on the perception of degraded stimuli has been examined in the context of incomplete or degraded pictures of common objects and in masking experiments, but not for degraded faces. Older adults are less accurate than younger adults at identifying fragmented pictures (Danziger & Salthouse, 1978), although the age-related reduction in degraded perception can be minimised if the older adults are able to view nondegraded versions of the stimuli prior to viewing the degraded version (Whitfield & Elias, 1992). The evidence for an increased vulnerability to stimulus degradation in the elderly is inconsistent. Some have found that the age-related difference in discrimination increases as fragmentation increases (Frazier & Hoyer, 1992), whereas others have reported no interaction of age and amount of stimulus degradation (Cremer & Zeef, 1987). Byrd and Moscovitch (1984) have reported that when masking is used to degrade perceptual representations of words, the type of mask used will determine whether age-related differences in identification will be found. That is, masks that merely add homogeneous noise to the visual stimuli may not differentially affect older adults but masks with more structure or patterns that would interfere more directly with object perception would result in a reduction in older adults' performance. There also is some evidence that perception of degraded stimuli is better when stimuli are presented to the right

hemisphere than when they are presented to the left hemisphere (Hellige, 1976; Jonsson & Hellige, 1986; Michimata & Hellige, 1987), but this asymmetry appears not to be affected by ageing (Byrd & Moscovitch, 1984; Dollinger, 1995). These behavioural results suggest that the discrimination ability of elderly observers under degraded viewing conditions may or may not be worse than that of their younger counterparts depending on the task demands.

The neural correlates of face perception in the elderly have not been studied in detail. One previous experiment found activation of areas in the fusiform gyrus during a face matching task in both young and old adults (Grady et al., 1994), consistent with the specialisation of these ventral visual areas for object perception (Haxby et al., 1994; Kanwisher, McDermott, & Chun, 1997; Sergent, Ohta, & MacDonald, 1992; Ungerleider & Mishkin, 1982). However, the older individuals, in comparison to the young adults, showed less activation of medial parts of visual cortex and greater activation in prefrontal cortex (Grady et al., 1994). In addition, face perception in these older adults was accompanied by increased feedback from prefrontal cortex to the occipitotemporal regions (Horwitz et al., 1995; McIntosh et al., 1994), suggesting an age-related alteration in the functional connectivity involved in face processing. In terms of degraded perception, we found in a previous study of degraded face discrimination in young adults (Grady et al., 1996) that there was a linear increase of activity in right prefrontal cortex as face degradation increased, along with a decline in activity in the occipitotemporal visual regions involved in face processing. An additional study of degraded picture identification in humans using event-related potentials found increasing negativity at 400 msec as the pictures became more incomplete (Stuss, Picton, Cerri, Leech, & Stethem, 1992), which was maximal over the frontal lobes. Thus, a direct relationship between stimulus discriminability and activity in both prefrontal cortex and visually responsive regions has been noted, and both these regions are affected by ageing.

In the current experiment we examined whether this relationship between face degradation and

brain activity would be altered in older adults. We hypothesised that older adults would be less accurate at discriminating the degraded faces and that the accompanying brain activity would reflect this difference, perhaps showing a smaller change in activity with increasing degradation or a more bilateral pattern of prefrontal activity similar to that seen in older subjects performing other types of cognitive tasks (Cabeza et al., 1997a; Cabeza, McIntosh, Tulving, Nyberg, & Grady, 1997b). Contrary to our expectations, we found that older adults showed a brain response to increasing face degradation that was indistinguishable from that seen in young adults, but that the relation between brain activity and the behavioural response was quite different in the two groups.

## METHODS

Ten young adults (mean age  $\pm$  SD,  $25 \pm 3$  yrs) and 10 old adults ( $66 \pm 4$  yrs) participated in the experiment. There were five males and five females in each group, and all participants, with the exception of one young female, were right-handed. All subjects were screened for health status to rule out any diseases that would compromise cerebral function (Duara et al., 1984), and none was taking any medication. The data from the young subjects have been published previously (Grady et al., 1996). All subjects with less than 20/20 vision uncorrected wore glasses during the scan, either their usual corrective lenses, or lenses custom-made to correct their vision for the viewing distance used during the scanning session (55cm).

The face stimuli used in this experiment (Grady et al., 1996) consisted of black-and-white photographs that had been altered by replacing a percentage of the image pixels with random gray values. The amount of degradation varied from none to 70% (i.e. 0%, 20%, 40%, 50%, 60%, 70%). All matching tasks utilised a forced-choice, two-alternative format, with each stimulus array consisting of three faces, one on the top of the array (the sample face) and two on the bottom (the choice faces). Subjects were instructed to press a button with their

right or left thumb to indicate whether the correct match was on the right or left side of the stimulus display. During the degraded conditions, only the two choice faces were altered. The tasks were subject-paced and the instructions emphasised accuracy rather than response speed. The control stimulus was a visual "noise" image that was the same size as the faces and similar in contrast and complexity (Grady et al., 1994). During the control tasks the noise pattern was presented using the same stimulus array that was used in the face matching tasks, with the noise pattern placed in each of the three stimulus positions. Subjects were instructed to alternate right and left hand responses with successive presentations of the control stimulus.

Participants underwent eight scans in total, two nonface control task scans (one at the beginning and one at the end of the scanning session), and the six face matching conditions. Each scan consisted of an injection of 37.5 mCi of  $H_2^{15}O$  and was separated from the following scan by 12 minutes. Scans were performed on a Scanditronix PC2048-15B tomograph (Uppsala, Sweden), which has a reconstructed resolution of 6.5mm in both transverse and axial planes. 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 minimised by using a thermoplastic mask that was moulded to each subject's head and attached to the scanner bed. Each task started 1 minute prior to isotope injection and continued throughout the scanning period. Scanning began when the radioactive count rate reached a threshold value in the brain, and continued for 4 minutes. Blood flow was calculated using a rapid least squares method (Carson et al., 1987; Holden et al., 1981).

Accuracy of face matching (per cent correct) and reaction time for correct responses were analysed with repeated measures ANOVAs with group as the independent factor and level of degradation as the within-subject factor. Both raw behavioural measures and measures adjusted for nondegraded face matching performance (using a ratio with nondegraded performance as the denominator) were analysed.

PET data were registered, spatially normalised to the Talairach and Tournoux atlas coordinate system (Talairach & Tournoux, 1988), and smoothed (to 10mm) using SPM95 (Frackowiak & Friston, 1994). The rCBF values were then proportionally scaled (each voxel to global flow for each subject). To examine brain activity during nondegraded face matching, compared to the control task, and the effect of increasing degradation on brain activity, rCBF was analysed using Partial Least Squares (McIntosh, Bookstein, Haxby, & Grady, 1996). Partial Least Squares (PLS) is a multivariate analysis that operates on the covariance between brain voxels and the experimental design to identify a new set of variables (so-called Latent Variables or LVs) that optimally relate the two sets of measurements. Two PLS analyses were carried out for both age groups combined to examine task effects and task by group interactions—one analysis that contrasted the nondegraded face matching task with the two control tasks, and one that contrasted the six face matching conditions (degraded and nondegraded). Prior to the PLS analyses, the overall group effect, which often is confounded by errors in registration between groups, was removed. To accomplish this, the rCBF value in each voxel for each subject was adjusted by regressing out the group main effect from each voxel, leaving only the residual variance due to the response of the brain to the tasks. We then used PLS to analyse the correlation of the brain voxel values with orthogonal contrasts coding for task and group by task interactions. Weights, which are either positive or negative and are known as saliences, are computed for each brain voxel and represent the contribution of that voxel to a given LV. Using these saliences, “brain scores” are then computed for each subject, which indicate the degree to which the pattern of activity identified by a LV is expressed in each subject in each condition. Plotting these brain scores by condition for each LV shows how rCBF in the brain areas that are identified by that LV changes across the experimental conditions.

Statistical significance was assessed by means of a permutation test (Edgington, 1980; McIntosh et al., 1996) to assign a probability value to each LV as

a whole. In the permutation test the data are randomly scrambled 500 times and the PLS analysis is recalculated to determine how frequently the scrambled data results in larger amounts of covariance accounted for than the original LVs, thus allowing an exact probability to be obtained for each LV. To determine the stability and reliability of the patterns identified by the LVs, the standard error of the saliences at each voxel were estimated through bootstrap resampling (Efron & Tibshirani, 1986). For PLS, this method provides an assessment of the precision of saliences (Sampson, Streissguth, Barr, & Bookstein, 1989). Saliences with values greater than twice their estimated standard error, i.e. with a salience/*SE* ratio  $\geq 2.0$ , were considered stable (Sampson et al., 1989), since these ratios are roughly analogous to *Z* scores (a *Z* score of 1.96 has  $P < .05$ , two-tailed). The local maximum of each stable region was defined as the voxel with the largest ratio within a 2cm cube centred on that voxel. Locations of these maxima are reported in terms of brain region, or gyrus, and estimated Brodmann area (BA) as indicated in the Talairach and Tournoux atlas.

A similar PLS analysis was used to examine the covariance between the behavioural measures and rCBF. For this analysis the adjusted behavioural measures (ratios to nondegraded performance) were used, so that only the degraded conditions were included (20%–70%). To make the brain values comparable to the behavioural ratios, the rCBF value at each voxel in each degraded condition was divided by the value at that voxel in the nondegraded condition. This type of PLS analysis is carried out on the correlation matrix of rCBF and behavioural measures rather than the task contrasts used for the analysis described above (Schreurs et al., 1997). Both behavioural measures (i.e. accuracy and RT) were included in this analysis so that we could determine whether rCBF was similarly or differentially correlated with these two measures within and across conditions. The saliences resulting from this analysis were submitted to the bootstrap procedure as described earlier. The behavioural PLS was carried out on the young and old adults separately, and only the first LV from each analysis will be presented here.

## RESULTS

## Behaviour

Performance by young and old adults on the face-matching tasks is shown in Table 1. There was a significant main effect of group on task accuracy ( $F = 26.4$ ,  $P < .001$ ), as well as a significant main effect of degradation ( $F = 60.2$ ,  $P < .001$ ). The interaction of degradation and group was not significant. Since the older adults were less accurate on the nondegraded face condition, the accuracy results also were analysed after the accuracy for each of the degraded conditions was divided by the accuracy in the nondegraded condition. The significant effects of task and group on these ratio values remained, although the group effect was much reduced in size (task  $F = 40.6$ ,  $P < .001$ ; group  $F = 4.8$ ,  $P < .05$ ). The only significant effect on reaction time was that of degradation condition, both for the raw measures ( $F = 29.0$ ,  $P < .001$ ), and for the ratio-adjusted RT measures ( $F = 17.5$ ,  $P < .001$ ).

## Task-related Changes in rCBF

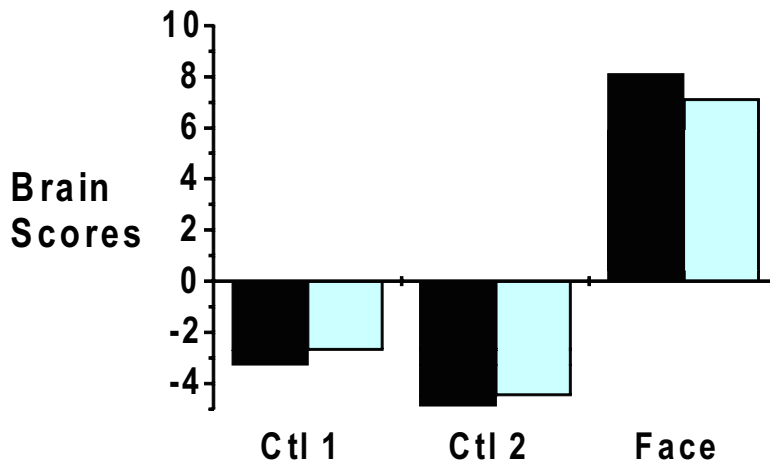
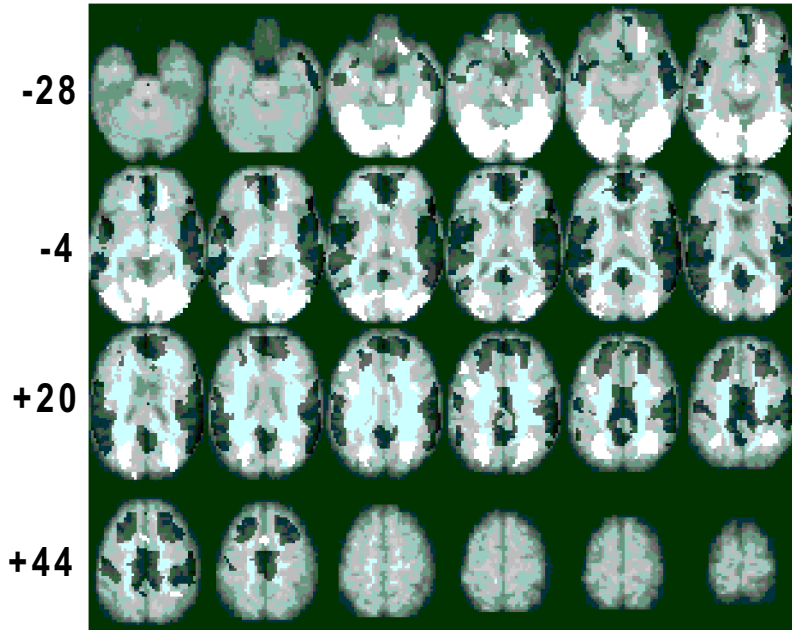
Comparison of rCBF during the nondegraded face-matching task with that during the control task was carried out to assess age-related differences in baseline face perception in the absence of any manipulation of the stimuli. The first brain activity pattern identified by this analysis ( $P < .0001$ ) revealed a number of brain areas with differential activity during face matching vs. the control tasks in both young and old adults (Fig. 1A and Table 2A). Increased rCBF in the areas with positive salience on this LV (seen in white in Fig. 1A) characterised the face matching conditions (i.e. those conditions in which subjects had positive brain scores), whereas increased activity in those areas with negative salience characterised the control tasks (those conditions in which subjects had negative brain scores). The areas with increased activity during face matching included bilateral extrastriate cortex, extending into the anterior fusiform gyrus in the right hemisphere, bilateral premotor cortex, right ventral prefrontal cortex, and left dorsolateral

**Table 1.** Performance on the Face Matching Tasks

|                         | Degradation Level |             |             |             |             |             |
|-------------------------|-------------------|-------------|-------------|-------------|-------------|-------------|
|                         | 0                 | 20%         | 40%         | 50%         | 60%         | 70%         |
| <i>Young Adults</i>     |                   |             |             |             |             |             |
| Raw Values <sup>a</sup> |                   |             |             |             |             |             |
| Accuracy (SD)           | 99 (1)            | 95 (5)      | 89 (7)      | 86 (8)      | 81 (10)     | 71 (10)     |
| RT (SD)                 | 2385 (839)        | 3087 (1039) | 3615 (1664) | 4053 (1588) | 4912 (1734) | 5546 (1958) |
| Adjusted <sup>b</sup>   |                   |             |             |             |             |             |
| Accuracy (SD)           |                   | 0.96 (0.04) | 0.90 (0.06) | 0.86 (0.08) | 0.81 (0.09) | 0.72 (0.09) |
| RT (SD)                 |                   | 1.31 (0.19) | 1.49 (0.30) | 1.73 (0.49) | 2.11 (0.56) | 2.50 (1.08) |
| <i>Old Adults</i>       |                   |             |             |             |             |             |
| Raw Values <sup>a</sup> |                   |             |             |             |             |             |
| Accuracy (SD)           | 90 (4)            | 83 (7)      | 74 (8)      | 69 (11)     | 69 (8)      | 58 (6)      |
| RT (SD)                 | 2681 (824)        | 3171 (1195) | 3286 (1183) | 3622 (1662) | 4651 (1558) | 5022 (1954) |
| Adjusted <sup>b</sup>   |                   |             |             |             |             |             |
| Accuracy (SD)           |                   | 0.93 (0.06) | 0.83 (0.11) | 0.77 (0.13) | 0.77 (0.09) | 0.65 (0.06) |
| RT (SD)                 |                   | 1.17 (0.19) | 1.25 (0.32) | 1.33 (0.33) | 1.75 (0.52) | 1.97 (0.89) |

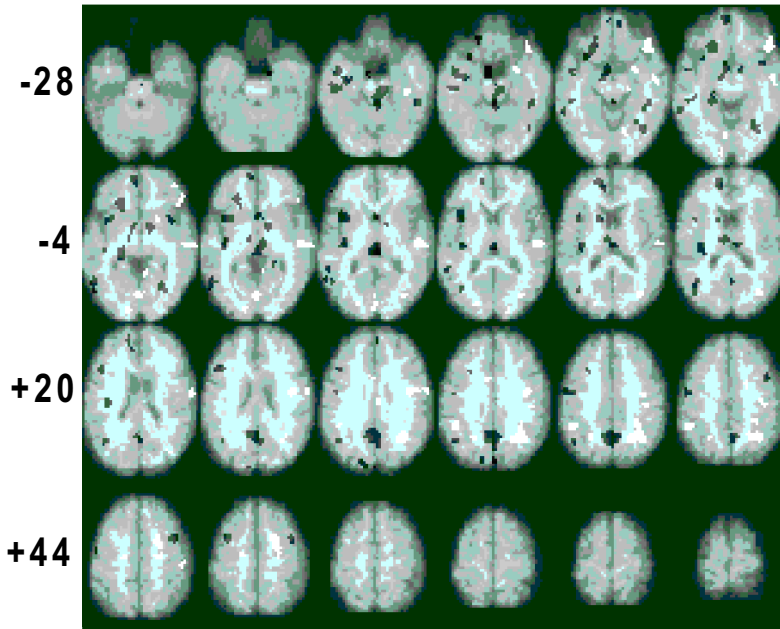
<sup>a</sup>Raw values: Accuracy is per cent correct, reaction time (RT) is in msec. <sup>b</sup>Adjusted for baseline face matching.

## A. Face Matching v. Control

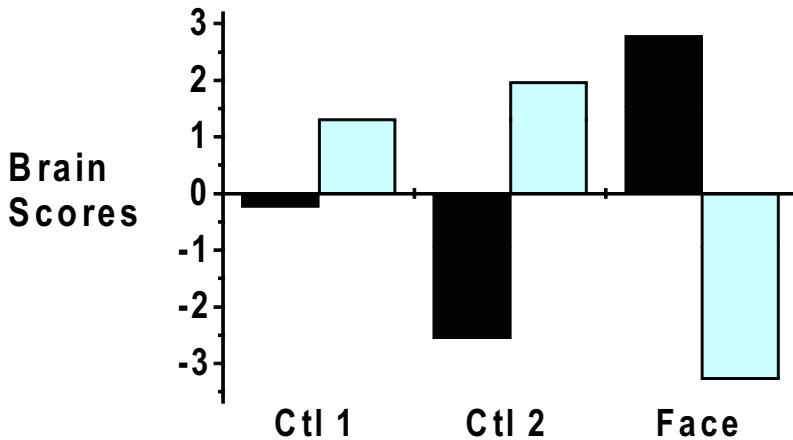


**Fig. 1.** Pattern of task contrasts and brain areas contributing to this pattern for two LVs from the comparison of nondegraded face matching to the control tasks (brain areas meeting the bootstrap criterion of salience/SE  $\geq 2.0$  are shown). The images at the top of the figure show the brain regions (plotted on a standard MRI) with positive saliences (shown in white) and negative saliences (shown in black) on the LVs. In this figure (and in figures following) the right side of the brain is shown on the right side of the images. The numbers to the left of each row of brain images indicate the level in mm relative to the AC-PC line of the leftmost image in each row. The graphs at the bottom of the figure show the mean brain scores plotted for each of the task conditions for young and old subjects separately. These scores are analogous to factor scores in a principle component analysis. The first LV shown on the left of the figure (A) identifies brain regions with greater activity during

## B. Task by Group Interaction



Young  
 Old



face matching or during the control. Increased rCBF in brain areas with positive saliences is found in those conditions where the mean brain score is positive (face matching), whereas the opposite pattern holds for regions with negative salience. On the right side of the figure is shown the third LV (B) which identified a task by group interaction. Regions with positive salience (resulting in positive brain scores) showed increased activity in young subjects during face matching, whereas regions with negative salience (resulting in negative brain scores) showed increased activity in older adults during face matching. The second LV from this analysis identified a time effect (i.e. from the first control task to the second which was always the last scan in the sequence) and is not presented here.

**Table 2.** Local Maxima of Regions with Differential Activity in Non-degraded Face Matching vs. Control

| Region, Gyrus               | Hem | BA   | X   | Y   | Z   |
|-----------------------------|-----|------|-----|-----|-----|
| <b>A. Face &gt; Control</b> |     |      |     |     |     |
| Prefrontal                  |     |      |     |     |     |
| GOB                         | R   | 11   | 16  | 18  | -20 |
|                             | L   | 11   | -12 | 34  | -20 |
| GFm                         | L   | 9    | -48 | 22  | 32  |
| Premotor (GPrC)             | R   | 6    | 26  | 2   | 28  |
|                             | L   | 6    | -36 | -6  | 28  |
| Thalamus                    | R   |      | 10  | -24 | -4  |
|                             | L   |      | -14 | -22 | 4   |
| Parietal (LPi)              | R   | 7/40 | 32  | -58 | 40  |
|                             | L   | 40   | -24 | -56 | 36  |
| Extrastriate                |     |      |     |     |     |
| GF                          | R   | 19   | 28  | -74 | -4  |
|                             | R   | 37   | 34  | -62 | -20 |
|                             | R   | 37   | 40  | -38 | -20 |
|                             | L   | 19   | -34 | -70 | -12 |
| GL                          | L   | 18   | -6  | -78 | -20 |
| Pcu                         | R   | 7/19 | 22  | -70 | 32  |
|                             | L   | 18   | -28 | -72 | 20  |
| <b>B. Control &gt; Face</b> |     |      |     |     |     |
| Prefrontal                  |     |      |     |     |     |
| GFd                         | R   | 9    | 6   | 46  | 32  |
|                             | L   | 10   | -10 | 58  | 12  |
| GF <sub>i</sub>             | R   | 45   | 50  | 18  | 8   |
| GF <sub>s</sub>             | R   | 8    | 18  | 26  | 44  |
|                             | L   | 8    | -18 | 26  | 44  |
| Cingulate (GC)              | R   | 32   | 8   | 36  | 0   |
|                             | M   | 24   | 2   | -14 | 40  |
|                             | L   | 23   | -6  | -56 | 12  |
| Premotor (GPrC)             | R   | 6    | 44  | 2   | 8   |
|                             | L   | 6    | -40 | -6  | 8   |
| Sensory (GPOC)              | R   | 3    | 46  | -20 | 40  |
|                             | L   | 3    | -56 | -8  | 24  |
| Temporal (GTM)              | R   | 22   | 42  | -34 | 4   |
|                             | R   | 21   | 46  | -10 | -12 |
|                             | L   | 21   | -50 | -38 | -4  |
|                             | L   | 39   | -48 | -62 | 20  |

Coordinates from regions (seen in Fig. 1) of at least 30 contiguous voxels. Coordinates and estimated

Brodmann's areas from Talairach and Tournoux (1988).

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.

Abbreviations: BA = Brodmann's area; Cu = cuneus; GC = cingulate gyrus; GF(s,m,i,d) = frontal gyrus (superior, middle, inferior, medial); GF = fusiform gyrus; GH = parahippocampal gyrus; GL = lingual gyrus; GOB = orbitofrontal gyrus; GO<sub>i</sub> = inferior occipital gyrus; GO<sub>m</sub> = middle occipital gyrus; GPOC = postcentral gyrus; GPrC = precentral gyrus; Gsm = supramarginal gyrus; GT(s,m,i) = temporal gyrus (superior, middle, inferior); GTT = transverse temporal gyrus; Hem = hemisphere; LPi = inferior parietal; Mid = midline ( $\leq 5$  mm from 0 point in X dimension); Pcu = precuneus.

prefrontal cortex (Table 2A). Increased activity also was seen during nondegraded face matching in bilateral parietal cortex and the posterior thalamus. Increased activity during the control tasks compared to face matching was found in anteromedial prefrontal cortex, cingulate gyrus, middle and inferior temporal cortex, sensorimotor cortex, and perisylvian regions (Fig. 1A and Table 2B). This pattern of activity characterised both young and old adults.

Another LV from this analysis ( $P = .004$ ) identified a task by group interaction (Fig. 1B). Young adults had greater activity during face matching relative to the control task, compared to older adults, in a number of right-hemisphere regions, including ventral premotor, ventral prefrontal, and superior temporal cortices. Bilateral activity in posterior extrastriate and parietal cortices also was greater in the young group during baseline face matching (Table 3A). The older group, on the other hand, showed greater activity during face matching, compared to younger adults, in mostly left hemisphere areas, such as prefrontal and temporal cortices, including the hippocampus, the insula, and the posterior thalamus (Fig. 1B and Table 3B). Bilateral activity during face matching was greater in old adults in anterior portions of the fusiform gyri, and dorsal premotor areas in the region of the frontal eye fields (Paus, 1996). In fact, most of the regions where young adults showed more activity during face matching in this interaction were in the right hemisphere, whereas most of the regions where old adults had greater activity were in the left hemisphere (Table 3). Some of the regions identified by this LV, such as right auditory cortex, where young adults showed greater activity during face matching, and posterior cingulate, where old adults showed greater activity, actually had reduced activity during face matching compared to the control task (compare the right and left images in Fig. 1). Thus, these group differences in activity patterns in these areas may reflect a difference in "deactivation" during the control task rather than an increased "activation" during face matching.

The analysis that examined the effect of increasing face degradation on rCBF resulted in one LV that was significant by permutation test ( $P < .0001$ ).



**Table 3.** Local Maxima of Regions with Task x Group Interaction (Non-degraded Face Matching vs. Control: Face > Control)

| Region, Gyrus          | Hem | BA    | X   | Y   | Z   |
|------------------------|-----|-------|-----|-----|-----|
| <b>A. Young Adults</b> |     |       |     |     |     |
| Prefrontal (GFi)       | R   | 11/47 | 38  | 24  | -12 |
| Cingulate (GC)         | R   | 24    | 20  | 2   | 48  |
| Motor/Premotor (GPrC)  | R   | 4     | 56  | -6  | 24  |
|                        | R   | 6     | 34  | -8  | 28  |
| Temporal (GTs)         | R   | 42/22 | 46  | -18 | 4   |
| <b>Parietal</b>        |     |       |     |     |     |
| Gsm                    | R   | 39    | 28  | -56 | 28  |
|                        | L   | 40    | -26 | -58 | 36  |
| LPi                    | L   | 40    | -42 | -46 | 36  |
| <b>Extrastriate</b>    |     |       |     |     |     |
| GL                     | L   | 18    | -8  | -74 | -8  |
| GOm                    | R   | 19    | 30  | -74 | 12  |
| <b>B. Old Adults</b>   |     |       |     |     |     |
| <b>Prefrontal</b>      |     |       |     |     |     |
| GOb                    | L   | 11    | -24 | 22  | -8  |
| GFd                    | L   | 10    | -8  | 56  | -8  |
|                        | L   | 9     | -16 | 48  | 16  |
| GFi                    | L   | 45    | -44 | 18  | 20  |
| <b>Premotor</b>        |     |       |     |     |     |
| GPrC                   | R   | 6     | 36  | 6   | 44  |
| GFm                    | L   | 6     | -52 | -8  | 40  |
| <b>Insula</b>          |     |       |     |     |     |
|                        | L   |       | -40 | 8   | 4   |
|                        | L   |       | -38 | -20 | 4   |
| <b>Thalamus</b>        |     |       |     |     |     |
|                        | L   |       | -10 | -16 | 16  |
| <b>Midbrain</b>        |     |       |     |     |     |
|                        | M   |       | 2   | -28 | -20 |
| <b>Cingulate</b>       |     |       |     |     |     |
|                        | M   | 23    | -4  | -56 | 28  |
| <b>Temporal</b>        |     |       |     |     |     |
| GTm                    | L   | 37    | -50 | -60 | 0   |
|                        | L   | 39    | -40 | -60 | 20  |
| GH                     | L   | 36    | -32 | -14 | -20 |
| Hipp                   | L   |       | -22 | -36 | -4  |
| <b>Extrastriate</b>    |     |       |     |     |     |
| GF                     | R   | 19    | 26  | -70 | -4  |
|                        | R   | 37    | 38  | -40 | -12 |
|                        | L   | 20    | -48 | -24 | -20 |

Coordinates from regions (seen in Fig. 1) of at least 30 contiguous voxels. Coordinates and Brodmann's areas from Talairach and Tournoux (1988). Abbreviations are the same as in Table 2.

This LV identified brain regions that showed a linear change in activity in response to increasing degradation of the faces (Fig. 2). Regions with increased activity (Table 4A) included an extensive area of right dorsolateral prefrontal cortex, smaller areas of medial and lateral prefrontal cortex in the left hemisphere, and a region encompassing the

**Table 4.** Coordinates of Local Maxima that Show Linear Changes in rCBF with Increasing Face Degradation in Young and Old Adults

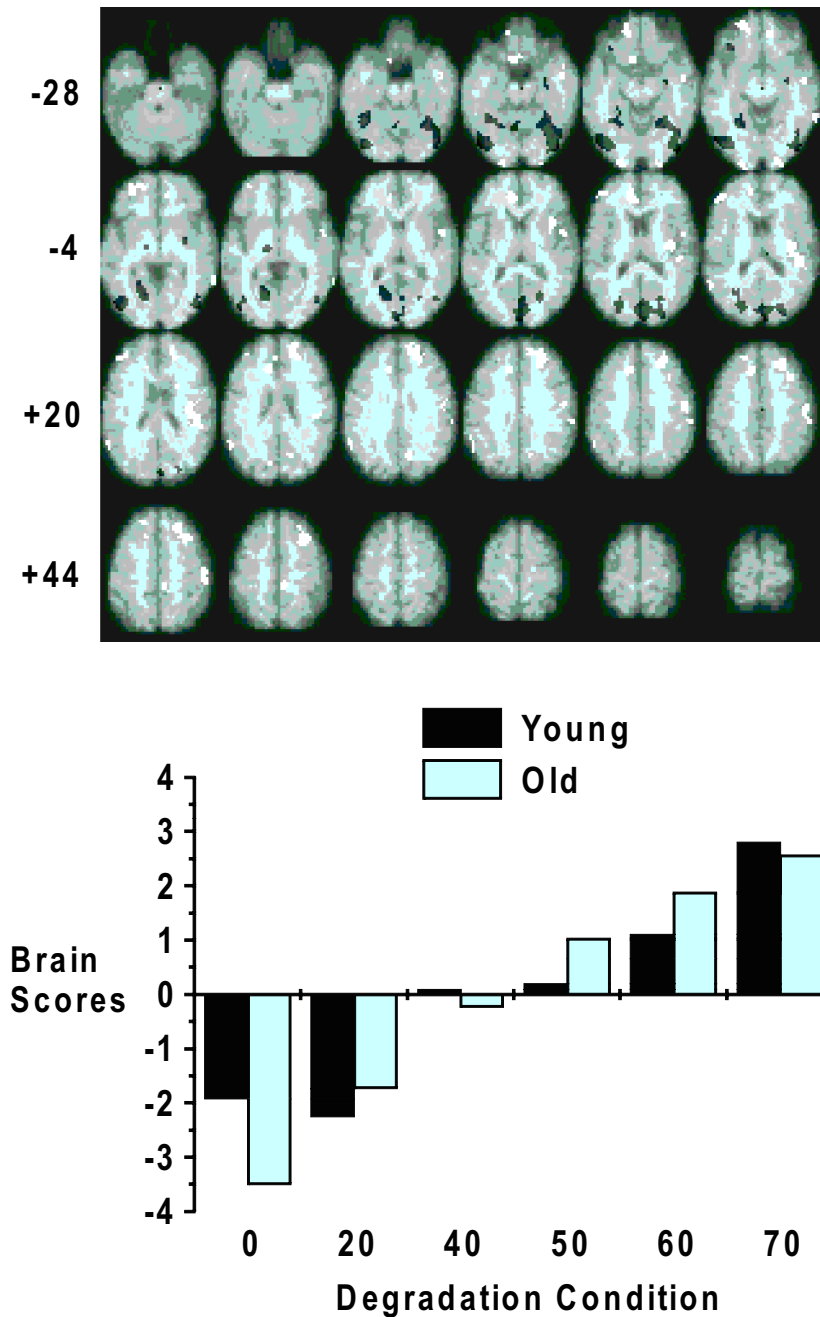
| Region, Gyrus       | Hem | BA    | X   | Y    | Z   |
|---------------------|-----|-------|-----|------|-----|
| <b>A. Increase</b>  |     |       |     |      |     |
| <b>Prefrontal</b>   |     |       |     |      |     |
| GOb                 | L   | 25    | -12 | 14   | -16 |
| GFd                 | R   | 9     | 14  | 46   | 24  |
|                     | L   | 10    | -16 | 44   | -8  |
| GFi                 | L   | 45/46 | -46 | 40   | 20  |
| GFm                 | R   | 8/9   | 20  | 34   | 36  |
|                     | R   | 8     | 28  | 20   | 44  |
| Cingulate (GC)      | L   | 32    | -12 | 36   | 8   |
| Insula              | R   |       | 28  | -14  | 16  |
| Sensory (GPOC)      | R   | 3     | 48  | -18  | 44  |
| Temporal (GTT)      | R   | 41/42 | 40  | -32  | 16  |
| Parietal (LPi)      | L   | 39    | -56 | -56  | 24  |
| <b>Extrastriate</b> |     |       |     |      |     |
| GF                  | L   | 18    | -22 | -102 | -12 |
| GTi                 | R   | 37    | 58  | -48  | -8  |
| <b>B. Decrease</b>  |     |       |     |      |     |
| <b>Extrastriate</b> |     |       |     |      |     |
| GOi                 | L   | 18    | -46 | -76  | -8  |
| GOm                 | R   | 18    | 22  | -84  | 16  |
|                     | L   | 18    | -22 | -82  | 16  |
| GF                  | R   | 19/37 | 28  | -60  | -16 |
|                     | L   | 19    | -22 | -62  | 0   |
| Cu                  | M   | 18    | -2  | -82  | 16  |

Coordinates from regions (seen in Fig. 2) of at least 30 contiguous voxels. Coordinates and Brodmann's areas from Talairach and Tournoux (1988). Abbreviations are the same as in Table 2.

right insula and auditory region. Several small areas of increase also were seen in extrastriate cortex, mainly in posterior and ventral regions. Decreases in brain activity with increasing face degradation were found in ventral and dorsal extrastriate cortex bilaterally, including medial prestriate regions (Table 4B). This pattern of rCBF change in response to face degradation was the same for both young and old adults (Fig. 2).

## Correlations of rCBF and Behaviour

The analysis of rCBF and behaviour was carried out only on the degradation conditions (20–70%) using the behavioural and rCBF measures that had been adjusted for the effect of the nondegraded



**Fig. 2.** Pattern of task contrasts and brain areas contributing to this pattern for the significant LV from the analysis contrasting all of the face matching tasks. Conventions are the same as in Fig. 1. The image at the top of the figure shows the brain regions with linear increases (positive saliences, shown in white) and decreases (negative saliences, shown in black) in rCBF as face degradation increased. In the graph at the bottom of the figure, the increase in brain scores from negative to positive can be seen for both young and old adults. This graph shows that the lower levels of degradation were characterised by increased activity in regions with negative salience (e.g. extrastriate cortex) whereas higher levels of degradation were characterised by increased activity in regions with positive salience (e.g. right prefrontal cortex).

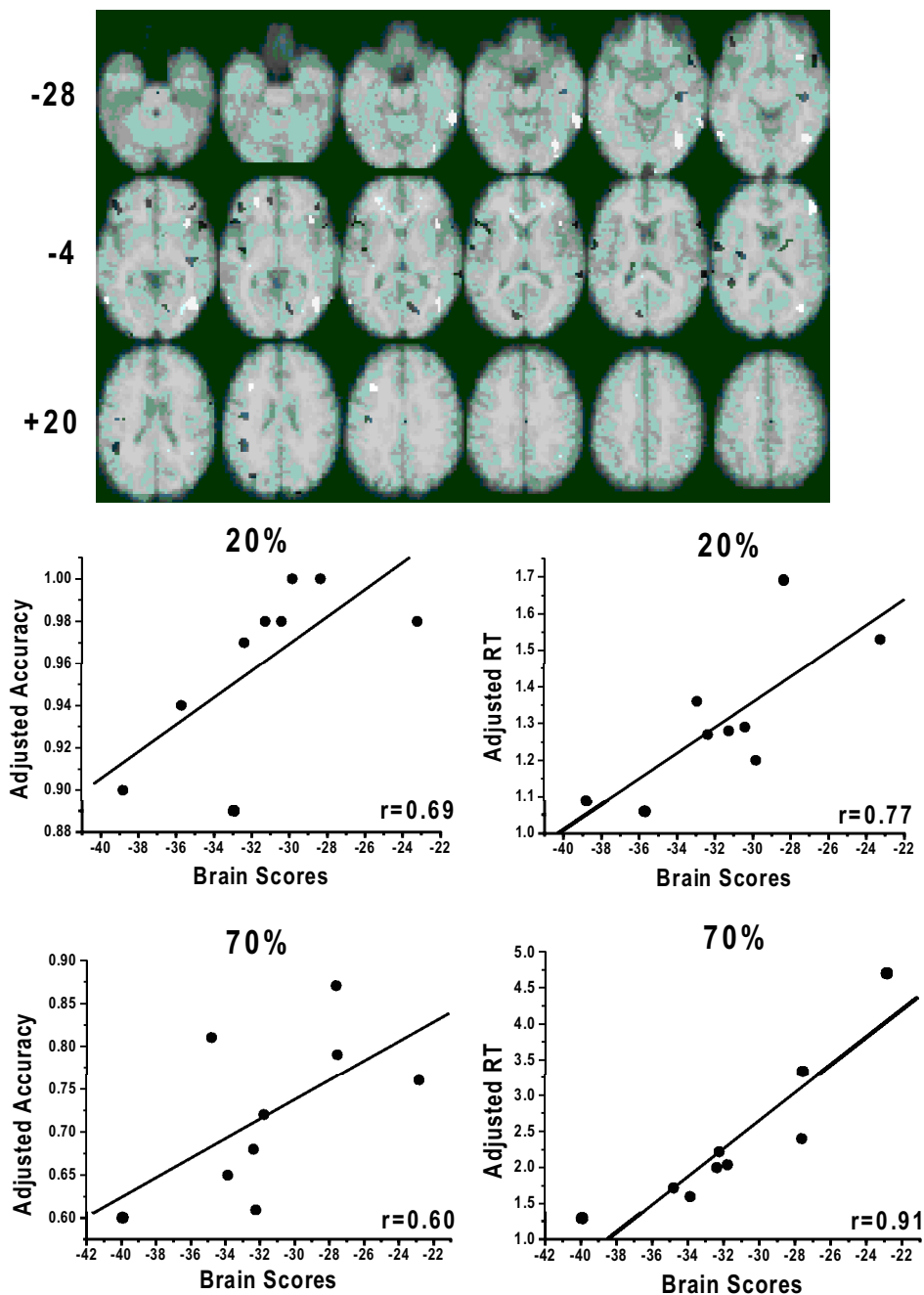
condition. Although *across* degradation conditions accuracy decreased and RT increased, *within* each condition there was a positive association between the adjusted measures for accuracy and RT in the young adults (correlations ranged from .41 to .84), and also in the old adults (although the correlations were somewhat lower, ranging from .13 to .60). Thus, one might expect that within each condition rCBF would be correlated similarly with both behavioural measures, i.e. either positively correlated with both or negatively correlated with both. The first LVs from the PLS analyses of rCBF and behavior showed just such a result in that a set of brain regions was identified where activity correlated positively with both accuracy and RT. In addition, these correlations were found to be similar across the conditions, indicating a common relation between brain activity and discrimination performance regardless of level of degradation. We will focus on those regions identified in the behavioural analysis that also showed differential activity during face matching compared to the baseline condition or showed a modulation of activity with increasing degradation, i.e. that reflected changes in stimulus input as well as behavioural output.

The results of the behavioural analysis are best assessed by examining the correlations between the behavioural measures and the brain scores from the analysis. Since the brain scores give an indication of the total contribution of all the brain areas participating in each LV, the relation of these scores to performance shows how increases or decreases of rCBF are related to behaviour. The first LV for both young and old adults (seen in Figs. 3 and 4, respectively) identified brain areas that had positive correlations of brain scores with both accuracy and RT measures over all the face matching conditions (range from .50 to .91 in young adults and from .13 to .97 in old adults). The scatterplots of brain scores and behavioural measures seen in Figs. 3 and 4 indicate that increased rCBF in the regions shown in white at the top of the figures (positive saliences resulting in more positive brain scores) was associated with an increase in both accuracy and RT (the 20% and 70% conditions are shown in the figures as representative of the associations seen across all conditions). Conversely, increased rCBF in the

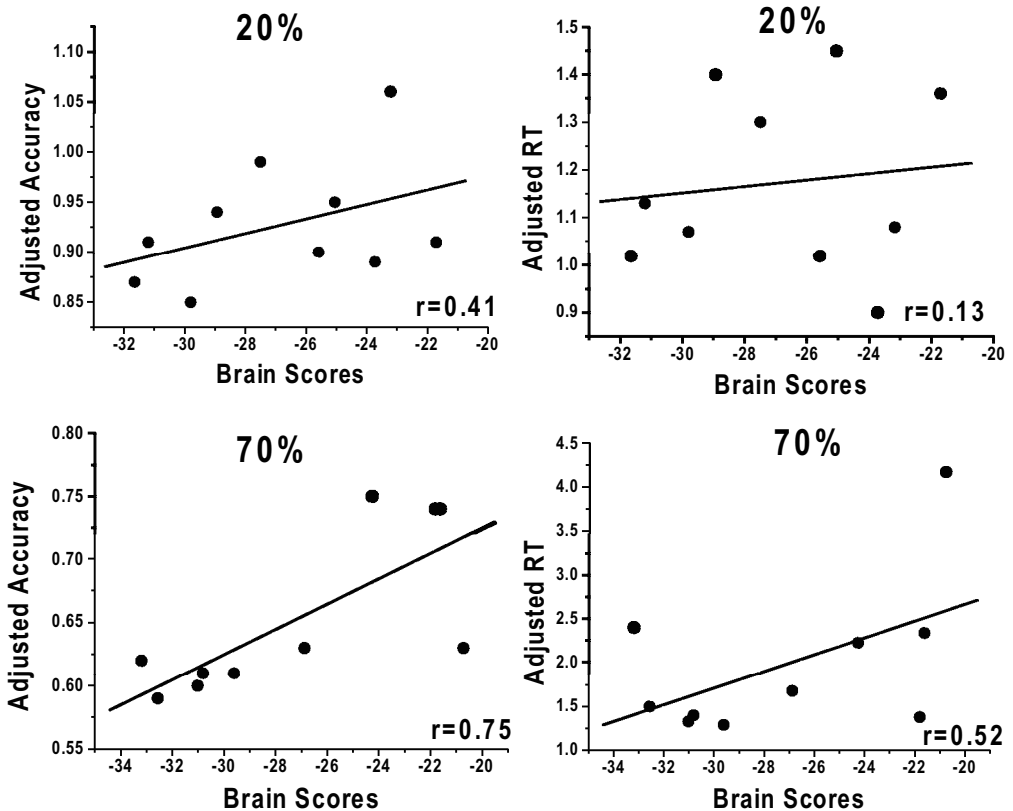
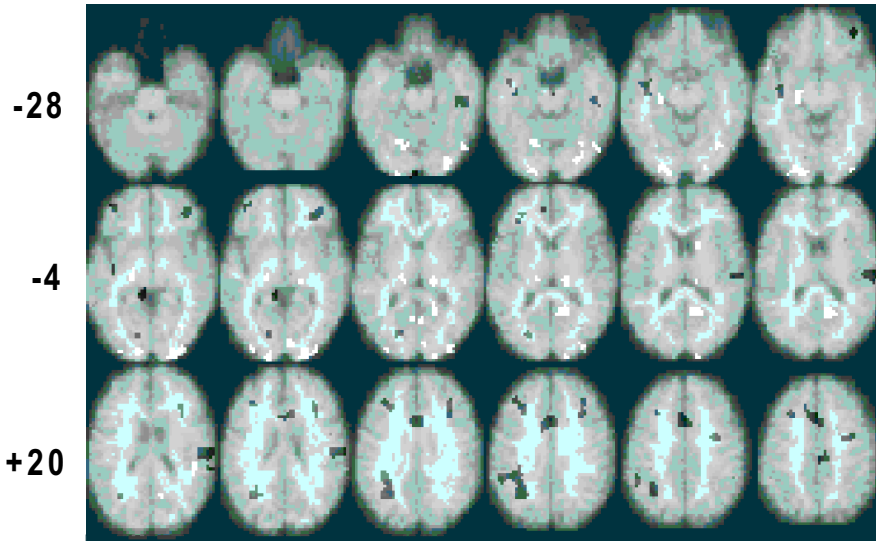
regions shown in black in Figs. 3 and 4 (negative saliences resulting in more negative brain scores) was correlated with a decrease in both behavioural measures.

The only regions where increased rCBF in young adults was associated with increased accuracy and RT (that also corresponded to regions with a task effect) were in extrastriate cortex, mainly in the right fusiform gyrus (Table 5A). All of these areas were similar in location to regions of extrastriate cortex that showed both increased activity in nondegraded face matching, compared to the control task, and a decrease in activity as face degradation increased (compare Fig. 3 to Fig. 1A). Several areas showed an association between increased rCBF and reductions in both accuracy and response times across all levels of degradation. These areas included regions of perisylvian cortex (Table 5B), and all showed decreased activity in nondegraded face matching compared to the control tasks (compare Fig. 1A and Fig. 3).

The first LV from the brain-behaviour analysis of the older adults identified brain regions with a common pattern of correlations across the conditions, similar to that seen in the young adults (Fig. 4), but the brain areas identified by this pattern were not the same as those seen in LV1 from the young group. The older group showed a correlation between increased rCBF in bilateral extrastriate cortex and both behavioural measures, as did the young group, but the extrastriate regions in the older adults were more posterior. In addition to extrastriate cortex, increased activity in the thalamus, posterior cingulate, and hippocampus was associated with increased accuracy and response times across all degraded conditions in the old adults (Table 5A). The occipital and thalamic areas were activated during face matching compared to the control tasks (compare Fig. 1A and Fig. 4), and the left thalamus also was more active during face matching in the old adults compared to the young adults (compare Fig. 1B and Fig. 4). In addition, the left hippocampal region showed more activation during face matching in the old adults compared to the young adults (see Figs. 1 and 4) as well as a positive correlation with behaviour. Four regions showed an association between increased



**Fig. 3.** The first LV from the behavioural correlation analysis of the young subjects' data (regions meeting the bootstrap criterion of salience/ $SE \geq 2.0$ ). The images at the top show the brain regions with positive (in white) and negative saliences (in black) on this LV on a standard MRI. Numbers indicate level of images relative to the AC-PC line as in Fig. 1. Plots of brain scores vs. accuracy and response time for the 20% and 70% conditions are shown at the bottom of the figure. The correlations are such that increased rCBF in regions with positive salience leads to more positive brain scores and an increase in both accuracy and RT. Increased rCBF in regions with negative salience is associated with reductions in both behavioural measures.  $N = 9$  in this figure due to missing behavioural data in one young participant.



**Fig. 4.** The first LV from the old subjects' behavioural analysis. Conventions for this figure are the same as for Fig. 2. Plots of brain scores vs. accuracy and response time for the 20% and 70% conditions are shown at the bottom of the figure. Increased rCBF in regions with positive salience leads to more positive brain scores and an increase in both accuracy and RT. Increased rCBF in regions with negative salience is associated with reductions in both behavioural measures across all degradation conditions.

**Table 5.** *Regions where rCBF is Positively or Negatively Correlated with Accuracy and Reaction Time*

| <i>A. Positively Correlated</i> |            |           |          |          |          |                    |
|---------------------------------|------------|-----------|----------|----------|----------|--------------------|
| <i>Region</i>                   | <i>Hem</i> | <i>BA</i> | <i>X</i> | <i>Y</i> | <i>Z</i> | <i>Task Effect</i> |
| <i>Young Adults</i>             |            |           |          |          |          |                    |
| <i>Extrastriate</i>             |            |           |          |          |          |                    |
| GF                              | R          | 19        | 38       | -68      | -4       | Face > Ctl, Dec    |
|                                 | R          | 37        | 52       | -42      | -20      | Face > Ctl, Dec    |
| GOM                             | L          | 19/37     | -54      | -62      | -4       | Face > Ctl, Dec    |
| <i>Old Adults</i>               |            |           |          |          |          |                    |
| <i>Extrastriate</i>             |            |           |          |          |          |                    |
| GF                              | L          | 18        | -22      | -92      | -12      | Face > Ctl, Inc    |
|                                 | L          | 19        | -18      | -64      | -16      | Face > Ctl         |
| GOi                             | R          | 18        | 30       | -92      | -4       | Face > Ctl         |
| Thalamus                        | R          |           | 14       | -28      | 4        | Face > Ctl         |
|                                 | L          |           | -16      | -24      | 4        | Face > Ctl, O > Y  |
| Hippocampus                     | L          |           | -22      | -26      | -8       | O > Y              |
| Cingulate (GC)                  | R          | 23/31     | 12       | -58      | 12       | Ctl > Face         |
| <i>B. Negatively Correlated</i> |            |           |          |          |          |                    |
| <i>Region</i>                   | <i>Hem</i> | <i>BA</i> | <i>X</i> | <i>Y</i> | <i>Z</i> | <i>Task Effect</i> |
| <i>Young Adults</i>             |            |           |          |          |          |                    |
| Premotor                        | L          | 6         | -54      | -4       | 12       | Ctl > Face         |
| Sensory                         | L          | 3         | -38      | -14      | 28       | Ctl > Face         |
| Temporal (GTs)                  | R          | 22        | 46       | 16       | -4       | Ctl > Face         |
| Parietal (LPi)                  | L          | 40        | -42      | -38      | 24       | Ctl > Face         |
| <i>Old Adults</i>               |            |           |          |          |          |                    |
| Prefrontal (GFm)                | L          | 9         | -38      | 32       | 32       | Ctl > Face         |
| Sensory                         | R          | 2         | 50       | -18      | 20       | Ctl > Face         |
| Insula                          | L          |           | -38      | -12      | -4       | O > Y              |
| Parietal (Gsm)                  | L          | 39        | -30      | -58      | 28       | Y > O              |

Coordinates from regions seen in Figs. 3 and 4. Coordinates and Brodmann's areas from Talairach and Tournoux (1988). Abbreviations are the same as in Table 2. Task Effect refers to the contrast in the task analysis (or analyses) in which a similar brain region was found to be active: Face > Ctl = greater activity during nondegraded face matching vs. the control tasks; Ctl > Face = greater activity during the control tasks vs. nondegraded face matching; O > Y = greater increase during nondegraded face matching in the old adults; Y > O = greater increase during nondegraded face matching in the young adults; Dec = decreasing activity with increasing face degradation; Inc = increasing activity with increasing face degradation.

rCBF and a reduction in both accuracy and RT regardless of degradation level in the older group (Table 5B). Similar to the pattern seen in the young adults, two of these areas showing negative correlations with behaviour, the left prefrontal and right sensory regions, were more active during the control task. The other two areas showed a task by group interaction, the insula being more active in the old adults during nondegraded face matching, and the parietal region being more active in the young adults.

To summarise the brain-behaviour results, the correlations between rCBF and the two behavioural measures were in the same direction, reflecting the fact that accuracy and RT covaried directly within each face degradation condition. However, although both young and old adults showed correlations between increased activity in visual areas of the brain and increased accuracy and RT across all degradation levels, these regions were not the same in the two groups. In young adults activity in the fusiform gyrus was associated with increases in behavioural measures whereas in the old adults positive correlations were found between performance and activity in a system of regions composed of posterior occipital cortex, the pulvinar region of the thalamus, posterior cingulate and the hippocampal region. Negative correlations between rCBF and behavioural measures were generally found in perisylvian cortex and regions near the central sulcus in both groups.

## DISCUSSION

The performance of young and old participants on these face matching tasks was notable in two respects. First, there was an age-related reduction in accuracy of face discrimination even in the nondegraded condition. This behavioural result differs somewhat from our previous work, in which we found equivalent performance in young and old adults on tasks of face matching (Grady et al., 1994). However, in that earlier study the face stimuli were taken from a standard test of face perception (Benton, 1990), in which the faces were photographed from different angles and under

varying lighting conditions, making matching of these faces more difficult for both young and older adults. This increase in task difficulty may have obscured any age-difference that might have been present. When using the current set of face stimuli, small but significant reductions in face matching accuracy in the older adults are observed, both in this experiment and in a previous one (Grady et al., 1995). Thus, when the face discrimination task is made easy, young adults perform almost at ceiling whereas older adults do not, although their performance is still quite good (90% or better).

The second interesting aspect of the behavioural data is that although the older adults were more susceptible to the effects of face degradation per se, the effect of *increasing* degradation was the same in both groups. Removing the influence of baseline face perception reduced the age difference in degraded performance but there was no significant interaction of age and amount of degradation on either accuracy or reaction time. This suggests that an age-related change in face processing per se accounted for most, but not all, of the reduction in accuracy seen during degraded face processing in these older adults, but the residual age-difference in degraded performance was not worsened by increasing the amount of stimulus degradation. This result is consistent with studies reporting equivalent changes in performance with stimulus degradation in young and old adults (Cremer & Zeef, 1987; Dollinger, 1995) or age  $\times$  degradation interactions on some tasks but not others (Byrd & Moscovitch, 1984). In addition, these behavioural results suggest that age-related changes in more complex tasks, such as perception of degraded stimuli, can be greatly influenced by perceptual changes at more basic levels of function.

### Brain Activity During Nondegraded Face Matching

Increased rCBF was found in both groups of subjects across widespread areas of ventral and dorsal extrastriate cortices when the nondegraded face-matching task was compared to the sensorimotor control task. Activation also was seen in premotor and parietal cortices, as well as in the thalamus. It is

interesting that the areas with increased activity during nondegraded face matching compared to the control task appear to include both the ventral and dorsal visual processing streams. That is, they include the fusiform regions and ventral prefrontal areas thought to comprise the ventral object identification system (Ungerleider & Mishkin, 1982), as well as parietal cortex and premotor regions considered to be part of the dorsal localisation or visuomotor system (Goodale, 1996; Ungerleider & Mishkin, 1982). The dorsal system has not been previously delineated to this degree during face matching (Haxby et al., 1994). Both ventral and dorsal streams may be more involved in this experiment because the stimuli used were larger than those used in our previous face matching experiments. This might have resulted in more eye movements or a greater degree of visuomotor activity, thus involving the dorsal stream to a greater extent.

In both groups, there were regions in sensory, medial prefrontal, and temporal cortices that showed reduced activity during face matching compared to the control task. Reduced activity in these areas has been noted previously in face perception and memory tasks (Clark et al., 1996; Grady et al., 1998; Haxby et al., 1994), and has been interpreted as a suppression of unattended modalities in order to focus attention on the attended visual modality. In addition, sensory and temporal regions, including auditory cortex, showed a linear increase of activity with increasing face degradation. We reported a similar result in an experiment on memory for faces in which the retention interval varied linearly from 1 to 21 seconds (Grady et al., 1998). Such a finding suggests that deactivation of these regions during visual tasks is not constant, but varies as the demands of the task vary, whether it be a perceptual task or a memory task, and may indicate a lessening of cross-modality suppression with increasing task difficulty.

Some of the regions with differential activity during face matching compared to the control task showed greater activity in one group or the other. For example, young adults had greater activity during face matching in prestriate, ventral prefrontal, and parietal cortices. Greater activity in prestriate cortex in younger adults compared to older adults

has been found previously during face matching (Grady et al., 1994) and was interpreted as a reduction in low-level visual processing in the older individuals. We have also noted greater right ventral prefrontal activation in young adults compared to old adults in a face memory task (Grady et al., 1998), indicating that young adults may have a stronger input into this frontal region from ventral visual stream regions during face processing in general and perhaps in other kinds of visual tasks. Activity in the parietal areas could be related to eye movements or to the visuomotor operations involved in making the response as noted earlier (Goodale, 1996; Petit et al., 1996; Zihl & Hebel, 1997). On the other hand, young adults also had greater activity in a region of premotor cortex associated with sequencing of finger movements (Boecker et al., 1998), which may reflect differences in the motor programming of the manual response. In general, greater activity in the right hemisphere of young adults during face matching, compared to the older adults, is consistent with our previous finding of right hemisphere dominance in this task (Horwitz et al., 1992; McIntosh et al., 1994). This finding, coupled with that of greater left-hemisphere activation in older adults, may indicate a more bilateral involvement of the brain in nondegraded face matching with increasing age.

Old adults had greater activity during nondegraded face matching than young adults in a number of brain areas that were previously found to differentiate these age groups. The areas in the fusiform gyri that were more active in older adults are similar in location to regions that are more activated in older adults during short-term memory for faces (Grady et al., 1998) as well as other face matching tasks (Grady et al., 1994). Given the role of this region in face processing (Haxby et al., 1994; Kanwisher et al., 1997; Sergent et al., 1992), the additional activity here in older adults suggests that a greater demand is placed on this area during face processing in the elderly, perhaps in response to the reduction in prestriate activity. Left prefrontal cortex also was more active in the old adults in this experiment as well as in several previous ones involving both face perception (Grady et al., 1994) and memory (Grady et al., 1998), as well as verbal



memory (Cabeza et al., 1997a; Madden et al., 1999). Prefrontal cortex in the left hemisphere has been implicated in visual encoding (Gulyas & Roland, 1995; Haxby et al., 1996), retrieval from semantic memory (Andreasen et al., 1995; Jennings, McIntosh, Kapur, Tulving, & Houle, 1997; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995), and visual working memory (Gold, Berman, Randolph, Goldberg, & Weinberger, 1996; Haxby, Ungerleider, Horwitz, Rapoport, & Grady, 1995). Older adults may thus rely more on associative strategies or those based on familiarity of the faces (Bartlett & Fulton, 1991), even when memory for the stimuli is not explicitly required, necessitating greater involvement of left prefrontal regions. The additional finding of greater activation of the hippocampal region in older adults supports this interpretation of strategy differences. In addition to the well-accepted role of this area in memory function (e.g. Squire, 1992), this region has been noted to be less active in older adults during both short-term memory for faces (Grady et al., 1998) and longer-term memory for faces (Grady et al., 1995). Increased activity in medial temporal regions in the elderly during face processing tasks not requiring memory may have an adverse impact on this region's ability to increment its activity level during memory processing as well as on our ability to detect such an increment.

### **Brain Activity During Degraded Face Matching**

The multivariate analysis used in this study identified brain areas with changes in activity directly related to increasing face degradation that were similar to, but more extensive than, those reported previously for the young adults using a univariate analysis (Grady et al., 1996). Areas of increased activity in right prefrontal cortex and decreased activity in ventral extrastriate cortex were essentially identical in both analyses, with the added finding in the present report that this pattern characterised old as well as young adults. The main difference is that the multivariate approach was able to identify additional regions that showed a change in rCBF with increasing degradation. Although our previ-

ous analysis in young adults suggested that right prefrontal cortex was most directly related to increasing stimulus degradation, the current analysis identified additional right-hemisphere regions, including temporal and parietal cortices, as well as left prefrontal cortex. A recent experiment (Barch et al., 1997) that compared brain activity during working memory tasks (using letter stimuli) in which memory load and stimulus degradation were manipulated separately, also identified right prefrontal regions that had increased activity related to stimulus degradation, although these were ventral to the right prefrontal areas related to degradation in our experiment. These two findings taken together suggest that the right hemisphere, and specifically the right prefrontal cortex, is important for degraded viewing tasks. However, our results also indicate that a role for left prefrontal cortex cannot be excluded. Left prefrontal cortex is activated during visual encoding (Haxby et al., 1996; Owen, Milner, Petrides, & Evans, 1996), so that increased rCBF in this area is consistent with increasing demand on complex visual analysis. Alternatively, the left prefrontal region has been implicated during a number of difficult tasks, including increasing memory load (Braver et al., 1997; Grasby et al., 1994; Haxby et al., 1995), noncanonical object perception (Kosslyn et al., 1994), and learning of a motor sequence compared to overlearned performance (Jenkins, Brooks, Nixon, Frackowiak, & Passingham, 1994). This region may be involved in monitoring or organising performance on difficult tasks regardless of the exact nature of the task. Also of interest is the increased activity in cingulate and parietal regions with increasing face degradation. A number of years ago Bauer (1984) hypothesised that these two areas, in conjunction with limbic regions, were responsible for covert face recognition in a patient with an occipitotemporal lesion who was prosopagnosic. Bauer suggested that the dorsal visual stream interacted with regions involved in emotion and autonomic functions, effectively bypassing the damaged occipitotemporal area that normally would have been part of this loop, resulting in the autonomic arousal that was observed in response to familiar faces. In a similar fashion, pari-

etal and anterior cingulate regions may participate in face recognition when activity in occipito-temporal regions is reduced temporarily, in this case via stimulus degradation.

Areas of decreased activity during degraded face matching are limited to ventral and dorsal extrastriate cortex, including the face-specific areas. This was true of the old adults as well as the young adults. This finding is consistent with the reduction in the number of stimuli easily recognisable as faces as degradation increases, and with the finding of reduced activity in face-selective neurons in monkeys during degraded face perception (Perrett et al., 1984; Rolls, Baylis, & Hasselmo, 1987; Rolls, Baylis, & Leonard, 1985). The lack of any age-related change in the pattern of degradation-related modulation of rCBF indicates that the basic response of the brain to face degradation does not change markedly with age. Indeed, our results suggest that differences in brain activity during baseline face matching far exceed any that might exist during degraded processing. However the way in which the brain's activity is related to behavioural output within the degradation conditions is markedly different in young and old adults.

### Changes in rCBF Related to Behaviour

The correlations between brain activity and performance on the degradation tasks were in the same direction for both accuracy and RT, reflecting the speed/accuracy trade-off in performance that was found within the degradation conditions. In the young adults the extrastriate areas showing positive correlations with both accuracy and RT across all degradation conditions were similar to those found with a more traditional correlational analysis in these young subjects (Grady et al., 1996). An interesting finding is that there was considerable overlap between those areas with a task-related change in activity and those areas whose activity predicted behaviour. Most of the task-related changes were from the comparison of nondegraded face matching to the control task, despite the fact that the influence of this nondegraded task was removed from both the behaviour and the brain measures prior to the correlational analysis. This pattern of

results suggests that performance on the degraded tasks in young adults can be predicted to a large extent by activity in areas involved in nondegraded face processing. In general increased activity in areas more active during baseline face processing (e.g. fusiform gyrus) was associated with better accuracy on the degraded tasks, although at a cost of slowed response times. Conversely, increased activity in those areas *less* active during baseline face processing (e.g. perisylvian areas) was associated with poorer accuracy on the degraded tasks. This pattern indicates that those participants who were best able to both activate face-processing regions in extrastriate cortex and deactivate regions not required for face processing were most accurate at discriminating the degraded stimuli.

Older adults, like younger adults, showed considerable overlap between those areas with a task-related change in activity and those areas whose activity predicts behaviour. The older adults showed a set of brain areas where activity was associated with increased accuracy and RT across all conditions, as did the young group, but the specific brain areas were different. The extrastriate regions where activity was correlated with increased accuracy and RT were in more posterior regions of occipital cortex in the old adults, rather than the middle portion of the fusiform gyrus as seen in young adults. In addition, increased activation of the thalamus and hippocampus was associated with higher accuracy and slower response times in the elderly. The left thalamus and hippocampus are particularly interesting since these areas were also more active during baseline face processing in the old adults compared to the young adults. This conjunction of results, i.e. a differential task effect and a positive relation to behaviour, is evidence that increased levels of activity in the old group in these areas may represent a compensatory mechanism. This group of regions—extrastriate cortex, posterior thalamus, medial temporal, posterior cingulate—is involved in visual processing and is highly interconnected with other visual areas (Baizer, Desimone, & Ungerleider, 1993; Olson & Musil, 1992; Suzuki & Amaral, 1994; Ungerleider & Mishkin, 1982; Van Essen, Anderson, & Felleman, 1992), suggesting an as yet unspecified

difference in how a face, and perhaps visual information in general, is processed in older adults.

## CONCLUSIONS

This experiment shows that degraded face perception is less accurate in older adults compared to younger adults. This difference is accounted for largely, but not entirely, by a reduction in nondegraded face perception. The rCBF analyses show that the age groups differ significantly in the brain activity patterns that mediate nondegraded face processing, but they do not differ in the brain response to degradation of the stimuli. Rather, the way in which brain activity is translated into the behavioural output is different in the older adults. Performance of both younger and older adults during the degraded tasks can be predicted to some extent by activity in regions that also participate in nondegraded face perception, but the regions whose activity is related to performance are not the same in the two groups. Although these results need to be replicated or supported with additional converging evidence, they are nevertheless suggestive of considerable functional plasticity in the older adult brain during face perception. Both the behavioural and brain data from this experiment indicate that there may be considerable impact of visual perceptual factors on more cognitively demanding tasks. This influence may reflect a processing inefficiency, a type of "internal degradation," that decreases discriminability and affects regional activity in a distributed fashion throughout the brain.

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