Age-related differences in brain activity underlying identification of emotional expressions in faces

Michelle L. Keightley,1,2,3 Kimberly S. Chiew,2 Gordon Winocur,3,4,6 and Cheryl L. Grady1,4,5

1Department of Occupational Science and Occupational Therapy, University of Toronto, 2Toronto Rehabilitation Institute, 3Rotman Research Institute, Baycrest Centre for Geriatric Care, 4Department of Psychology, 5Department of Psychiatry, University of Toronto, Toronto, and 6Department of Psychology, Trent University, Peterborough, Ontario, Canada

We used fMRI to explore brain activity in young and old adults, while they viewed and labeled faces expressing different emotions as well as neutral expressions. Older adults had significantly greater difficulty identifying expressions of sadness, anger and disgust than young adults. Both groups performed at ceiling for happy expressions. The functional neuroimaging data revealed that both young and old adults recruited a pattern of activity that distinguished happy expressions from all other expressions, but the patterns were age-specific. Older adults showed increased activity in ventromedial prefrontal cortex, lingual gyrus and premotor cortex for happy expressions, whereas younger adults recruited a more widely distributed set of regions including the amygdala, ventromedial prefrontal cortex, lateral prefrontal regions and bilateral inferior parietal and superior temporal areas. Conversely, younger adults showed more activity in the dorsal anterior cingulate for other types of expressions, and older adults had more activity in dorsal cingulate, as well as middle and inferior frontal gyri, somatosensory cortex, insula and middle temporal regions. These results support previous research demonstrating age differences in brain activity during emotional processing, and suggest possible age-related differences in cognitive strategy during identification of happy faces, despite no effect of age on this ability.

Keywords: aging; emotion; fMRI; faces

Social cognition has been defined as the ability to interpret and predict others’ behavior in terms of their beliefs and intentions, and to interact in complex social environments and relationships (Baron-Cohen et al. 2000). The ability to understand and respond to the emotional content and cues present in the environment and to remember emotional information are integral parts of social cognition (Grady and Keightley, 2002; Adolphs, 2003). The amygdala is thought to be a critical component of a network of regions involved in social cognition, particularly for the processing of emotions in faces (Gobbini and Haxby, 2007). Lesions to the amygdala disrupt this ability (Adolphs et al., 1994, 1999; Anderson and Phelps, 2000). Consistent with lesion work, functional neuroimaging studies in young adults have found amygdala activation when negative face expressions are viewed, particularly fear (Breiter et al., 1996; Morris et al., 1996; Whalen et al., 1998b; Blair et al., 1999; Pessoa et al., 2002; Anderson et al., 2003). Increased amygdala activity also has been observed in response to positive emotional stimuli, although less consistently (Hamann et al., 2002; Winston et al., 2003; Yang et al., 2003; Zald, 2003). More recently, a patient with bilateral amygdala damage (S.M.) who showed impaired ability to detect fear, demonstrated normal performance once she was directed to look at the eyes when judging the facial expression. This latter finding suggests a more general role for the amygdala in directing attention to social and emotional cues (Vuilleumier, 2005).

The cognitive appraisal of visually complex emotional stimuli also is a critical component of social cognition, and is thought to be mediated in part by occipital cortex (Kosslyn et al., 1996; Reiman et al., 1997; Morris et al., 1998; Sprengelmeyer et al., 1998; Taylor et al., 1998; Lane et al., 1999; Paradiso et al., 1999; Phan et al., 2002). Prefrontal cortex also appears to play a general role in attention to emotion and emotional appraisal (Drevets and Raichle, 1998; Ochsner et al., 2002; Cunningham et al., 2004) and is often active during tasks of emotional processing (Lane et al., 1997a, b, c; Reiman et al., 1997). Emotional tasks also involve the anterior cingulate, particularly when some cognitive component, in addition to emotion perception, is added to the task (e.g. gender identification or recognition of emotional stimuli, Taylor et al., 1998; Whalen et al., 1998a; Bush et al., 2000; Keightley et al., 2003). It has been suggested (Phan et al., 2002) that the anterior cingulate and medial prefrontal cortex, together with their extensive connections to subcortical limbic structures, may represent an interaction zone between affect and cognition.
Finally, the insula is thought to be critically involved in perceiving disgust (Phillips et al., 1997; Sprengelmeyer et al., 1998; Calder et al., 2000; Anderson et al., 2003), likely due to its role in visceral and somatosensory responses (Adolphs, 2002).

The effect of aging on social cognition has received considerable interest in recent years, particularly the effect of age on perceiving emotions in faces. In one early study, McDowell et al. (1994) found that older adults identified happy expressions as accurately as younger adults, but they were less accurate at identifying negative and neutral expressions. Similar results have since been reported by a number of other investigators, with an age reduction in labeling negative expressions and an age preservation in labeling happy expressions the most consistent findings (Oscar-Berman et al., 1990; McDowell et al., 1994; Bros gol and Weisman, 1995; MacPherson et al., 2002; Phillips et al., 2002; Calder et al., 2003; Keightley et al., 2006).

In addition, older adults show a decreased ability to detect threat from faces, compared to young adults (Ruffman and Edge, 2006). Moreover, the age reduction in labeling negative expressions is independent of general age-related cognitive changes in processing speed, basic face processing abilities, and reasoning about non-face stimuli (Sullivan and Ruffman, 2004; Keightley et al., 2006).

Consistent with the behavioral differences, initial neuroimaging studies have demonstrated age-related alterations of activity in the amygdala and other emotion-related areas. Reduced amygdala activity in older adults when viewing negative faces, as well as reduced activity in occipital and parietal regions when viewing positive faces, compared to young adults, have been reported (Iidaka et al., 2002; Gunning-Dixon et al., 2003; Fischer et al., 2005). An age reduction in amygdala activity has been reported for negative pictures, as well (Mather et al., 2004). On the other hand, older adults have more activity in medial and lateral prefrontal cortex when viewing emotional faces (Gunning-Dixon et al., 2003), particularly negative ones (Tessitore et al., 2005). This increased prefrontal activity is interesting in light of similar findings of increased prefrontal activity in elderly individuals during non-emotional tasks (Grady and Craik, 2000; Cabeza, 2002). Given the presumed roles for prefrontal cortex in emotion processing mentioned above, these data suggest that older adults rely more on cognitive appraisal of emotional faces than do younger adults.

To the best of our knowledge, no imaging experiment has assessed the ability of older and younger adults to label a broad range of emotional expressions. Thus, the purpose of the current study was to explore neural activity associated with the perception and labeling of multiple facial expressions in young and old adults, so that we could examine the neural processes associated with older adults’ preservation for labeling happy expressions, as well as those underlying reductions in labeling negative expressions. In addition, we used an analytic approach that emphasizes whole-brain patterns of activity, rather than focusing on individual brain regions. As happy faces are identified with high accuracy regardless of age and cultural background (Biehl et al., 1997), and are recognized more rapidly than negative expressions (Kirit and Endo, 1995), we expected to see patterns of activity unique to happy expressions in both young and older adults. In addition, based on previous neuroimaging data, we expected older adults to show different patterns of brain activity when labeling emotional expressions, involving reduced amygdala activity and greater prefrontal and anterior cingulate activity, particularly for negative faces.

**METHODS**

Participants in this experiment were 10 young adults (five men, five women) and 11 older adults (six women, five men; Table 1). All participants were Caucasian, except for two of the younger adults who were Asian. Participants were right-handed, with the exception of one young adult who was left-handed, and all gave informed consent in accordance with the ethics committees of Baycrest and Sunnybrook Health Sciences Centre. Participants were screened to rule out a history of psychiatric, neurological or other medical illness that might compromise cognitive function, or a history of substance abuse. We also assessed personality using the NEO Five Factor Inventory (Costa and McCrae, 1997) and emotional awareness using the 20-item Toronto Alexithymia Scale (TAS-20, Bagby et al., 1994). Alexithymia is a personality construct that includes difficulty identifying and describing feelings and difficulty distinguishing between feelings and the bodily sensations of emotional arousal (Parker et al., 1999). Mood was assessed using the Positive and Negative Affect Schedule (PANAS, Watson et al., 1988) and mental status with the Mini Mental Status Examination (Folstein et al., 1975). Younger adults had slightly more education than the older adults,

### Table 1 Demographic and behavioral measures

<table>
<thead>
<tr>
<th>Variable</th>
<th>Young</th>
<th>Old</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (years)</td>
<td>27.2 (2.4)</td>
<td>69.6 (9.2)</td>
</tr>
<tr>
<td>Education (years)</td>
<td>19.0 (2.3)</td>
<td>16.3 (3.0)</td>
</tr>
<tr>
<td>MMSE</td>
<td>29.7 (0.5)</td>
<td>28.9 (1.1)</td>
</tr>
<tr>
<td>Vocabulary</td>
<td>23.0 (4.3)</td>
<td>23.4 (3.8)</td>
</tr>
<tr>
<td>TAS-20</td>
<td>38.0 (7.0)</td>
<td>38.8 (8.3)</td>
</tr>
<tr>
<td>PANAS positive</td>
<td>31.8 (6.8)</td>
<td>36.4 (5.5)</td>
</tr>
<tr>
<td>PANAS negative</td>
<td>12.5 (1.6)</td>
<td>12.7 (2.8)</td>
</tr>
<tr>
<td>Face expression labeling</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Happy</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td>Surprise</td>
<td>0.92 (0.12)</td>
<td>0.95 (0.11)</td>
</tr>
<tr>
<td>Neutral</td>
<td>0.90 (0.16)</td>
<td>0.86 (0.18)</td>
</tr>
<tr>
<td>Anger</td>
<td>0.83 (0.19)</td>
<td>0.62 (0.18)*</td>
</tr>
<tr>
<td>Disgust</td>
<td>0.85 (0.18)</td>
<td>0.54 (0.24)*</td>
</tr>
<tr>
<td>Fear</td>
<td>0.78 (0.19)</td>
<td>0.68 (0.30)</td>
</tr>
<tr>
<td>Sad</td>
<td>0.83 (0.21)</td>
<td>0.61 (0.24)*</td>
</tr>
</tbody>
</table>

*Significant age difference, *P* < 0.05.

Values are means with s.d. in parentheses. Labeling measures are proportion correct.
changes (Ogawa et al., 1993), acquired with a single-shot T2*-weighted pulse sequence with spiral readout (TR = 2000 ms; TE = 40 ms; flip angle = 80°; effective acquisition matrix = 64 × 64 × 26; FOV = 20 cm; 26 slices; slice thickness = 5.0 mm).

Image analysis
Image preprocessing was performed using the Analysis of Functional Neuroimages software package (Cox, 1996). Time series data were spatially co-registered to correct for head motion using a 3D Fourier transform interpolation. Each volume in the time series was aligned to an early fiducial volume from the first imaging run in the scanning session. The alignment parameters were computed by an iterative weighted least squares fit to the reference volume. The peak range of head motion was less than 1.3 mm for all subjects. Motion corrected images were then spatially normalized to an fMRI spiral scan template generated from 30 subjects scanned locally. This template was registered to the MNI template used by SPM99. The transformation of each subject to the spiral template was achieved using a 12-parameter affine transform with sinc interpolation as implemented in SPM99, and smoothed with a Gaussian filter of 6 mm full-width-at-half-maximum (FWHM) to increase the signal-to-noise ratio. The initial 10 image volumes in each run, in which transient signal changes occur as brain magnetization reaches a steady state, were excluded from all analyses. The resulting voxel size after processing was 4 × 4 × 4 mm3.

For statistical analysis we used a multivariate approach, partial least squares, or PLS (McIntosh et al., 1996, 1999), in order to identify whole brain patterns of activity that varied across the emotion conditions. PLS operates on the covariance between brain voxels and the experimental design to identify latent variables, or LVs (similar to principal components), that optimally relate the two sets of measurements. In using PLS, we did not specify contrasts across conditions or groups in advance; rather, the algorithm extracts LVs explaining the covariance between conditions and brain activity, in order of the amount of covariance explained (with the first LV accounting for the most covariance). Each LV identifies a pattern of differences in brain activity across the conditions and specifies which brain voxels show this effect. Each brain voxel has a weight, known as a salience, which is proportional to the covariance of activity with the task contrast on each LV. Multiplying the BOLD contrast value in each brain voxel for each subject by the salience for that voxel, and summing across all voxels gives a ‘brain’ score for each subject on a given LV.

The PLS analysis examined activity across the face conditions in both young and old adults, allowing us to determine patterns of brain activity that differed across groups as well as across the emotion conditions. Data from the contempt condition were not included in either
Performance on the labeling task collected prior to the scans (Table 1) was analyzed with a repeated measures of analysis of variance (ANOVA), with age group as the between-subject factor and emotion condition as the within-subject factor. Scores for happy faces were not included in this analysis, as both groups showed perfect identification of these faces. For the remaining conditions, there was a significant main effect of emotional expression, \( F(5,95) = 6.0, P < 0.001 \), and the main effect of age was significant \( F(1,19) = 9.4, P < 0.01 \). However, the interaction of age and emotion also was significant, \( F(5,95) = 2.5, P < 0.05 \). To examine this interaction we tested simple main effects for each emotion (except happy and contempt). Compared to younger adults, older adults had reduced identification of anger \( F(1,19) = 6.7, P < 0.02 \), disgust \( F(1,19) = 10.7, P < 0.01 \), and sadness \( F(1,19) = 5.4, P < 0.05 \). Identification of surprise, fear and neutral expressions did not differ between the groups \( (F_s < 1) \).

In the analysis of fMRI data, LV1 \( (P < 0.002) \) revealed brain activity that differentiated happy expressions from all other expressions in young adults (Figure 1B), but did not distinguish the face expressions in older adults (Figure 1C). When young adults identified happy expressions, activity was increased in a widely distributed set of brain regions, including ventromedial prefrontal cortex, anterior and posterior cingulate gyrus, left postcentral gyrus, and bilateral middle frontal gyri (Figure 1A and Table 2). Other brain regions demonstrating increased activity for happy faces bilaterally included the cuneus, precuneus, inferior parietal lobe and superior temporal gyrus. Activity was decreased for happy expressions and/or increased during the other conditions only in the left dorsal anterior cingulate gyrus (Table 2). No changes in amygdala activity were noted using a cluster size of 10 voxels; however, smaller clusters of increased activity for happy faces were noted in the right amygdala (X: 24, Y: -8, Z: -24, ratio = 4.5 at TR4, 4 voxels) and in the left hemisphere in a region extending into both the amygdala and hippocampus (X: -24, Y: -16, Z: -24, TRs 2-7, ratio = 5.7 at TR5, 5 voxels, Figure 2).

LV2 \( (P < 0.02) \) differentiated happy expressions from other expressions only in the older adults (Figure 3). In old adults, happy expressions, and those of disgust to a lesser extent, were associated with increased activity in ventromedial prefrontal cortex, lingual gyrus and bilateral premotor cortex (Table 3). For the other negative expressions and neutral expressions, increased activity was seen in a large number of areas, including dorsal anterior cingulate, middle and inferior frontal gyri, somatosensory cortex, middle temporal gyr and the insula. No activity changes were noted in the amygdala in older adults, even after lowering the cluster size criterion.

Although the patterns of activity distinguishing happy faces differed in young and older adults, there appeared to be some regions where both groups had increased activity.
In the ventromedial PFC (Prefrontal Cortex) and lingual gyrus, there was overlap in the areas showing increased activity for happy faces in the two groups (Figure 4). In addition, decreased activity for happy faces, compared to other expressions, was found in very similar regions of dorsal anterior cingulate cortex in the two groups (for a further discussion of overlapping regions and differential timing of activations of young and old adults, please see Supplementary Material including Figures 5 and 6).

Finally, as neither of the patterns described earlier identified any differences for those emotions where older adults performed more poorly than the younger adults, we carried out three additional analyses directly comparing these emotions (anger, disgust and sadness) to the other emotions (except for happy) to look for differences in activity between the age groups. None of these analyses

### Table 2 Brain regions where activity differentiates happy from all other expressions in young adults (LV1)

<table>
<thead>
<tr>
<th>Region</th>
<th>BA</th>
<th>X</th>
<th>Y</th>
<th>Z</th>
<th>Ratio</th>
<th>TRs*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Happy &gt; Other Conditions</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R Orbitofrontal cortex</td>
<td>11</td>
<td>12</td>
<td>32</td>
<td>−16</td>
<td>−6.14</td>
<td>3,6</td>
</tr>
<tr>
<td>R Middle frontal gyrus</td>
<td>10</td>
<td>28</td>
<td>44</td>
<td>20</td>
<td>−6.23</td>
<td>3</td>
</tr>
<tr>
<td>R Middle frontal gyrus</td>
<td>10</td>
<td>32</td>
<td>56</td>
<td>8</td>
<td>−4.53</td>
<td>3,4,6,7</td>
</tr>
<tr>
<td>L Superior frontal gyrus</td>
<td>8</td>
<td>−24</td>
<td>40</td>
<td>44</td>
<td>−4.55</td>
<td>3</td>
</tr>
<tr>
<td>Medial frontal gyrus</td>
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<td>0</td>
<td>68</td>
<td>4</td>
<td>−8.59</td>
<td>3</td>
</tr>
<tr>
<td>L Medial frontal gyrus</td>
<td>6</td>
<td>−4</td>
<td>−4</td>
<td>56</td>
<td>−6.52</td>
<td>3,4,5,6</td>
</tr>
<tr>
<td>R Ventral anterior cingulate</td>
<td>25</td>
<td>8</td>
<td>24</td>
<td>−12</td>
<td>−4.42</td>
<td>2,3,5,6,7</td>
</tr>
<tr>
<td>R Insula</td>
<td>28</td>
<td>8</td>
<td>0</td>
<td>−5.87</td>
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<td></td>
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<tr>
<td>L Cuneus</td>
<td>17, 19</td>
<td>24</td>
<td>−72</td>
<td>8</td>
<td>−6.43</td>
<td>5</td>
</tr>
<tr>
<td>L Cuneus</td>
<td>19</td>
<td>−28</td>
<td>−88</td>
<td>28</td>
<td>−5.53</td>
<td>5,6</td>
</tr>
<tr>
<td>L Precuneus</td>
<td>31, 7</td>
<td>−4</td>
<td>−52</td>
<td>36</td>
<td>−5.65</td>
<td>3,4,5</td>
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<tr>
<td>R Precuneus</td>
<td>18, 7</td>
<td>20</td>
<td>−72</td>
<td>24</td>
<td>−4.69</td>
<td>2,3,5,7</td>
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<tr>
<td>L Lingual gyrus</td>
<td>17</td>
<td>−20</td>
<td>−72</td>
<td>−12</td>
<td>−6.12</td>
<td>3,4,5,7</td>
</tr>
<tr>
<td>R Inferior parietal lobe</td>
<td>40</td>
<td>60</td>
<td>−32</td>
<td>32</td>
<td>−5.53</td>
<td>3</td>
</tr>
<tr>
<td>L Postcentral gyrus</td>
<td>2</td>
<td>−60</td>
<td>−24</td>
<td>32</td>
<td>−5.26</td>
<td>3,4,5</td>
</tr>
<tr>
<td>R Superior temporal gyrus</td>
<td>22</td>
<td>60</td>
<td>−4</td>
<td>−4</td>
<td>−6.39</td>
<td>4</td>
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<td>L Superior temporal gyrus</td>
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<td>−20</td>
<td>4</td>
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<td>4</td>
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<td>L Posterior cingulate</td>
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<td>−16</td>
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<td>36</td>
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<tr>
<td>Happy &lt; Other Conditions</td>
<td>32</td>
<td>−8</td>
<td>24</td>
<td>40</td>
<td>4.59</td>
<td>2,3</td>
</tr>
</tbody>
</table>

*TRs where area is reliable; If more than one TR is listed, the TR in bold and underlined is the TR where the ratio was maximal.
R = Right; L = Left; BA = Brodmann’s area; Ratio = bootstrap ratio indicating reliability of each voxel (the largest ratio across the TRs is reported in the table). 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. Coordinates are in MNI space.

Fig. 2 (A) A region of the left amygdala/hippocampus where young adults had increased activity during labeling of happy expressions, shown on a mean sagittal image from the young adults (Y = −24, TR5). (B) The graph shows percent signal change (from baseline) in this region for all conditions in young adults.

Fig. 3 (A) Areas from LV2 (P = 0.02) with differential activity across emotional expressions are shown on the average structural MRI from the old group. Labels under each image refer to the TR from which the data were taken and the level relative to the AC–PC line. Red brain areas had increased activity during labeling happy expressions in old adults, and disgust expressions to a lesser extent, and blue areas had more activity during labeling of the other expressions. (B) Plot of mean brain scores for all conditions in young adults, who showed little contribution to this pattern. (C) Plot of mean brain scores across the expression conditions in old adults. The mean brain scores for happy and disgust expressions diverge from the other emotions as early as the first TR (2–4 s poststimulus onset).
resulted in significant LVs; however, there were a few regions from each that showed reliable bootstrap ratios. These can be found in Supplementary Table 4.

**DISCUSSION**

In this experiment, we measured brain activity associated with identifying a broad range of emotional face expressions. Consistent with the highly accurate identification of happy faces generally seen in adults, and found here, the main pattern of brain activity in both age groups distinguished happy faces from those expressing all other emotions. Our results also are in line with previous reports of age differences in brain activity associated with processing emotional faces. Although some areas, such as ventromedial PFC and lingual gyrus, were active for happy faces in both groups, young adults additionally activated the amygdala, lateral PFC, posterior cingulate, temporal and parietal regions. In contrast, lateral PFC and temporal regions were active in the older adults when labeling emotions other than happiness. The lack of significant findings that characterize differences between young and old adults during negative emotional processing is surprising in light of previous studies (i.e. Gunning-Dixon et al., 2003; Iidaka et al., 2002) and behavioral results indicating decreased performance for older adults. However, this may be related to methodological differences. In particular, because we examined brain activity across all the basic emotions, we were able to identify the

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**Table 3** Brain regions where activity differentiates happy and disgust from all other expressions in old adults (LV2)

<table>
<thead>
<tr>
<th>Region</th>
<th>BA</th>
<th>X (right/left)</th>
<th>Y (anterior/posterior)</th>
<th>Z (superior/inferior)</th>
<th>Ratio</th>
<th>TRs*</th>
</tr>
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<tbody>
<tr>
<td>Happy and Disgust &gt; Other Conditions</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R Medial frontal gyrus</td>
<td>10</td>
<td>4</td>
<td>52</td>
<td>-4</td>
<td>4.67</td>
<td>2</td>
</tr>
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<td>R Lingual gyrus</td>
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<td>4</td>
<td>-60</td>
<td>-4</td>
<td>5.44</td>
<td>2</td>
</tr>
<tr>
<td>R Precentral gyrus</td>
<td>6</td>
<td>56</td>
<td>-8</td>
<td>28</td>
<td>4.35</td>
<td>3</td>
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<td>12</td>
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<td></td>
<td></td>
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<tr>
<td>L Dorsal anterior cingulate</td>
<td>24/32</td>
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<td>-5.61</td>
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<td>40</td>
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<td>52</td>
<td>-8</td>
<td>-5.92</td>
<td>3,5</td>
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<tr>
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<td>28</td>
<td>-8</td>
<td>-7.50</td>
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<tr>
<td>R Middle frontal gyrus</td>
<td>46</td>
<td>44</td>
<td>40</td>
<td>16</td>
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<td>3,5</td>
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<tr>
<td>L Middle frontal gyrus</td>
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<td>8</td>
<td>36</td>
<td>-8.62</td>
<td>6,7</td>
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<td>-28</td>
<td>48</td>
<td>-10.29</td>
<td>7</td>
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<td>L Precentral gyrus</td>
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<td>L Superior frontal gyrus</td>
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<td>48</td>
<td>-4.79</td>
<td>4</td>
</tr>
<tr>
<td>R Superior temporal gyrus</td>
<td>22</td>
<td>40</td>
<td>-40</td>
<td>20</td>
<td>-4.32</td>
<td>4,6</td>
</tr>
<tr>
<td>R Middle temporal gyrus</td>
<td>21</td>
<td>44</td>
<td>-36</td>
<td>0</td>
<td>-6.45</td>
<td>6</td>
</tr>
<tr>
<td>L Middle temporal gyrus</td>
<td>21</td>
<td>-40</td>
<td>44</td>
<td>4</td>
<td>-4.44</td>
<td>2,6,7</td>
</tr>
<tr>
<td>R Middle temporal gyrus</td>
<td>39</td>
<td>36</td>
<td>-72</td>
<td>16</td>
<td>-6.55</td>
<td>5,6,7</td>
</tr>
<tr>
<td>L Thalamus</td>
<td>-20</td>
<td>-32</td>
<td>4</td>
<td>-9.58</td>
<td>7</td>
<td></td>
</tr>
</tbody>
</table>

*TRs where area is reliable; If more than one TR is listed, the TR in bold and underlined is the TR where the ratio was maximal.
R = Right; L = Left; BA = Brodmann’s area; Ratio = bootstrap ratio indicating reliability of each voxel (the largest ratio across the TRs is reported in the table). 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. Coordinates are in MNI space.

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Fig. 4 (A) Two regions of medial cortex where both young and older adults showed increased activity during labeling of happy expressions are shown on a mean image from the older adults. Regions were defined by determining those voxels where both young adults (TR 4) and older adults (TR 2) showed reliable activity. (B) Plots of percent signal change (from baseline) in the ventromedial PFC region with maximal overlap (X = 0, Y = 56, Z = -4) for all conditions in young and old adults. (C) Plots of percent signal change (from baseline) in the lingual gyrus region with maximal overlap (X = -4, Y = -60, Z = -4) across the expression conditions in young and old adults.
dominant patterns of brain activity characterizing the process of labeling a broad range of emotions, shedding new light on the functional neuroanatomy of emotional face processing and how this may be modulated by age.

**Neural correlates of identifying facial expressions in young adults**

Most neuroimaging studies have found amygdala activation in young adults when viewing negative faces (Breiter et al., 1996; Morris et al., 1996; Whalen et al., 1998b; Blair et al., 1999; Critchley et al., 2000; Pessoa et al., 2002; Anderson et al., 2003). We found increased activity in small regions of the amygdala bilaterally in the younger adults, but for happy faces, not negative ones. This is surprising, given the evidence that the amygdala is activated by negative facial expressions. On the other hand, it is not entirely unexpected as increased amygdala activity has been found also for positive faces (Hamann et al., 2002; Pessoa et al., 2002; Winston et al., 2003; Yang et al., 2003; Zald, 2003). Indeed, a recent study suggested that both right and left amygdala play a role in processing a wide range of emotional expressions, not just negative ones (Shaw et al., 2005). A recent model of amygdala function proposes that the right amygdala mediates autonomic responses to emotional stimuli whereas the left mediates conscious cognitive appraisal of emotional stimuli (Glascher and Adolphs, 2003). Based on this model, our results suggest that in young adults, happy faces engage both autonomic responses (via the right amygdala) and cognitive evaluation (via left amygdala engagement).

The pattern of brain activity that characterized happy faces in young adults also included a number of other regions previously shown to be active during emotional processing, such as ventromedial PFC and somatosensory cortex. For example, ventromedial PFC is interconnected anatomically with the amygdala (Amaral et al., 1992) and is involved in emotional decision making (Cicerone and Tanenbaum, 1997; Bechara et al., 1999; Price, 1999; Winston et al., 2003). It was shown recently (Lewis et al., 2005) that ventromedial PFC was activated during encoding of positive words and this activity was associated with later memory for these words, in line with our finding of more activity to happy faces. Our result also is consistent with a model of ventral PFC function that ascribes a role for ventromedial PFC in assessing and representing reward (O’Doherty et al., 2001; Kringlebch and Rolls, 2004). Our results suggest that ventromedial PFC is engaged for processing the primary reward properties of happy faces, perhaps in conjunction with activity in the right amygdala. Somatosensory activity during labeling of happy faces is consistent with the somatic marker hypothesis (Damasio, 1996) which states that people identify emotions in others by simulating these emotions in themselves via involvement of somatosensory cortex (Adolphs et al., 2000). The role of the posterior cingulate in emotion is not entirely clear, but the frequent activation of this region in studies of either emotion or autobiographical memory (Maddock, 1999) suggests that it may integrate these two functions. Increased activity in visual cortex during happy face identification, such as we found in the lingual gyrus, is consistent with other work showing modulation of visual regions during emotional tasks (Morris et al., 1998; Anderson et al., 2003) or when participants are viewing personally-relevant faces (Gobbini et al., 2004). Finally, the dorsal anterior cingulate is thought to mediate monitoring and error checking during a variety of cognitive tasks (Bush et al., 2000; Carter et al., 2001; Paus, 2001), so that reduced activity in this region for happy faces likely reflects a reduced need for these processes, when the expression can be easily labeled. Thus, we were able to identify a widespread group of regions whose combined activity facilitates happy face labeling and that reflects the multiple processes that are likely recruited for this purpose.

**Age differences in identifying emotional expressions**

Older adults were able to identify happy expressions with the same accuracy as younger adults, and showed a pattern of brain activity that distinguished happy expressions from the others, as was found for the younger adults. This pattern in the older group was similar in some ways to that seen in the young, including increased activity in ventromedial PFC and lingual gyrus, and decreased activity in dorsal anterior cingulate. These similarities indicate that the processes subserved by these regions for the identification of happy faces changes little with age. One explanation for this type of preserved processing of positive emotions by older adults is that they have more experience with emotional regulation and have learned to emphasize positive emotions over negative ones (Carstensen et al., 2003). However, it is not yet possible to know whether this is due to a positive motivational bias that affects brain activity, or to a spared ability to engage a distinct set of brain areas when a happy face is encountered, which could influence motivational factors.

In addition to some similarities, there were notable differences in the brain activity associated with processing face expressions in the young and old adults, including the fact that older adults showed no reliable modulations of activity in the amygdala. This is consistent with other studies showing an age reduction in this region (Iidaka et al., 2002; Gunning-Dixon et al., 2003), although other work would have suggested more amygdala activity for positive stimuli, in older adults compared to younger adults (Mather et al., 2004). A number of studies have now shown that task demands can influence activity in the amygdala when participants process emotional stimuli (Bush et al., 1998; Vuilleumier et al., 2001; Ochsner et al., 2002; Keightley et al., 2003), and it is likely that these demands will also influence age differences in how this region responds to emotional stimuli. Therefore, differences across studies in task demands may account for some of the variability in results;
nevertheless all studies to date, including the current one, are consistent in that age differences are found in amygdala activity. This suggests that older adults’ behavioral responses to emotional stimuli are mediated by age differences in the brain’s basic response to these stimuli.

Our data also indicated that there are age differences in the neural correlates of emotion beyond those seen in the amygdala. Older adults demonstrated a more widely distributed pattern of activity for negative and neutral expressions, compared to younger adults, which included increased activity in bilateral middle frontal and temporal regions, as well as somatosensory cortex. Increased activity in some of these regions, such as somatosensory cortex, was seen in response to happy expressions in young adults. As noted earlier, activity in this region may indicate that individuals rely on simulating emotions observed in other people to identify those emotions (Adolphs, 2002), and the age difference seen here suggests that older adults, unlike younger adults, may rely on this strategy for emotions other than happy. Increased prefrontal activity in older compared to younger adults during emotional processing was found in earlier studies (Iidaka et al., 2002; Mather et al., 2004), and we found differences here as well. In our study, these frontal differences were seen not so much in terms of degree, but in terms of which emotions elicited this frontal activity. That is, younger adults activated the middle frontal gyri when identifying happy expressions, whereas older adults activated middle and inferior frontal gyri when identifying neutral and most negative expressions. Although these differences cannot be directly related to their ability to identify the expressions (e.g. there were no age differences in the identification of neutral faces), they do suggest that younger and older adults utilize different brain networks for identifying emotions in faces, similar to findings of increased prefrontal activity in elderly individuals during non-emotional tasks (Grady and Craik, 2000; Cabeza, 2002).

It was surprising to find that the pattern of neural activity found for happy expressions in older adults also was associated with faces expressing disgust, and the reason for this is not clear. This finding could be related to evidence that older adults are sometimes better at identifying expressions of disgust than are younger adults (Calder et al., 2003), although in the current study expressions of disgust were identified with less accuracy by older compared to younger adults. Nevertheless, a similar brain pattern for disgust and happy faces, which are always easily identified by older adults, lends some support to the idea that the ability to recruit this pattern may benefit both types of expression recognition.

One limitation of the current study that should be noted is that the faces used in the labeling task have been standardized in younger adults across a variety of cultures (Biehl et al., 1997), but not in older adults. Indeed, when we began the study there were no face stimulus sets for which norms were available from old adults. Although no data are available regarding valence or arousal ratings in older adults for all of the faces used here, we have obtained ratings for a large stimulus set of emotional and neutral faces, which includes some of the faces used in the current experiment (Grady et al., 2007). These ratings did not differ significantly with age, suggesting that the age differences in brain activity observed in the current study were not due to age differences in the perceived intensity of the emotion or arousal to the faces. Nevertheless, it is clear that collecting normative data from older adults on labeling specific emotions would be useful for future work. Furthermore, it is unclear what influence labeling age-congruent faces would have on the current findings. As the stimulus set contained primarily young and middle-aged adults, future research should examine younger and older adults’ accuracy for rating emotional expressions portrayed by older adults.

CONCLUSIONS
We found that both young and older adults identified happy facial expressions with high accuracy, consistent with other work in this field (Kiriti and Endo, 1995; Leppanen and Hietanen, 2004; Suzuki et al., 2006). Recently, Suzuki et al. (2006) found that happy face recognition is independent of all other emotions, using a technique that controls for effects of task difficulty, and a recent MEG study found that viewing happy faces resulted in a larger amplitude of a face-specific evoked component compared to either faces expressing disgust or neutral faces (Lewis et al., 2003). This evidence, taken together with our fMRI results, suggests that the perception of happy face expressions may be distinct on a neural level and that this leads to a behavioral advantage in recognizing these faces. Although some regions such as ventromedial PFC were active for happy faces in both groups, the overall patterns for happy faces differed with age and this pattern was less specific in older adults, being also engaged in response to expressions of disgust. In addition, age differences were found in the amygdala and prefrontal cortex. Taken together the results suggest that older adults may rely on different cognitive strategies to identify both positive and negative emotional expressions in faces.

SUPPLEMENTARY DATA
Supplementary data are available in SCAN online.

Conflict of Interest
None declared.

REFERENCES
Adolphs, R., Damasio, H., Tranel, D., Cooper, G., Damasio, A.R. (2000). A role for somatosensory cortices in the visual recognition of emotion as
revealed by three-dimensional lesion mapping. Journal of Neuroscience, 20, 2683–90.


