Temporal Cortex Activation in Humans Viewing Eye and Mouth Movements

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We sought to determine whether regions of extrastriate visual cortex could be activated in subjects viewing eye and mouth movements that occurred within a stationary face. Eleven subjects participated in three to five functional magnetic resonance imaging sessions in which they viewed moving eyes, moving mouths, or movements of check patterns that occurred in the same spatial location as the eyes or mouth. In each task, the stimuli were superimposed on a radial background pattern that continually moved inward to control for the effect of movement per se. Activation evoked by the radial background was assessed in a separate control task. Moving eyes and mouths activated a bilateral region centered in the posterior superior temporal sulcus (STS). The moving check patterns did not appreciably activate the STS or surrounding regions. The activation by moving eyes and mouths was distinct from that elicited by the moving radial background, which primarily activated the posterior-temporal-occipital fossa and the lateral occipital sulcus—a region corresponding to area MT/V5. Area MT/V5 was also strongly activated by moving eyes and to a lesser extent by other moving stimuli. These results suggest that a superior temporal region centered in the STS is preferentially involved in the perception of gaze direction and mouth movements. This region of the STS may be functionally related to nearby superior temporal regions thought to be involved in lip-reading and in the perception of hand and body movement.

Key words: extrastriate cortex; eye movement; mouth movement; temporal lobe; superior temporal sulcus; gaze direction

Face recognition and analysis of facial expression form an important part of everyday interaction for humans and other primates. Electrophysiological studies in humans have demonstrated that discrete regions within the fusiform gyrus respond preferentially to faces and that stimulation of these regions can lead to transient prosopagnosia (Allison et al., 1994a). Neuroimaging data have provided further support for the role of ventral occipitotemporal cortex and, in particular, the fusiform gyrus in face perception (Sergent et al., 1992a; Haxby et al., 1994; Puce et al., 1995, 1996; Clark et al., 1996; Kanwisher et al., 1997; McCarthy et al., 1997). A close correspondence of ventral regions activated by faces in neuroimaging and electrophysiological studies has been recently demonstrated in the same individuals (Puce et al., 1997a). Activation by faces is not, however, limited to ventral occipitotemporal cortex. For example, in previous neuroimaging studies, we have shown discrete foci of activation to faces in lateral temporal cortex, particularly in the right hemisphere (Puce et al., 1995, 1996). We have also recorded event-related potentials (ERPs) sensitive to faces directly from lateral temporal cortex (Puce et al., 1997a).

Studies in nonhuman primates have suggested a functional differentiation of regions responsive to faces. Face-sensitive neurons are found within monkey inferior temporal (IT) cortex and within the superior temporal sulcus (STS) (Desimone, 1991; Gross, 1992; Perrett et al., 1992; Rolls, 1992). However, neurons within the STS are also sensitive to gaze and head direction and to face parts (Perrett et al., 1985, 1992; Yamane et al., 1988; Hasselmo et al., 1989). Some cells in the STS also respond to moving views of the head and body (Perrett et al., 1990) and to “biological motion” (Oram and Perrett, 1994) using point-light displays (Johansson, 1973).

It is possible that a similar functional distinction exists between ventral and lateral regions responsive to faces in humans. ERPs recorded directly from ventral cortex, primarily the fusiform gyrus, are larger to full faces than to isolated eyes (Allison et al., 1994b). By contrast, ERPs recorded over the lateral temporal scalp are larger to isolated eyes than to full faces (Bentin et al., 1996). Neuropsychological studies also suggest that portions of the temporal lobe are sensitive to face parts. For example, some patients with temporal lobe lesions are deficient in determining gaze direction, whereas others can no longer lip-read (Campbell et al., 1986; Perrett et al., 1988). Taken together, these results suggest the existence of neuronal systems sensitive to face parts located in lateral occipitotemporal cortex, in addition to face-perception mechanisms located in ventral occipitotemporal cortex.

In this study, we investigated the cortical activation patterns of subjects viewing faces in which the eyes repeatedly changed their direction of gaze or the mouth opened and closed. The results demonstrate that a region of superior temporal cortex, located primarily in the STS, is activated preferentially by moving eyes and mouths.

A preliminary report of these results has appeared (Puce et al., 1997b).

MATERIALS AND METHODS

Subjects. Eleven right-handed, neurologically normal subjects (six males) with an average age of 33.7 (range, 25–47) years participated in these studies. All subjects gave their informed consent for a protocol approved...
Experimental tasks. There were six experimental tasks (Fig. 1, top panel). Each consisted of two subtasks (A and B) that alternated throughout each imaging run as described previously (Puce et al., 1995, 1996). The duration of each subtask was 6 sec (Fig. 1, bottom panel). Fifteen AB cycles were presented during the 192 sec duration of each imaging run. Each task was replicated four times; i.e., four imaging runs were acquired. Two of these runs began with subtask A (ABAB . . .), and two runs began with subtask B (BABA . . .). The starting order was counterbalanced across imaging runs.

In the EYES task, one of two possible faces (male or female) was continuously present during the duration of the imaging run. In this and all other tasks, the male and female faces were used on alternate runs. The faces were in color and were superimposed on a radial background pattern consisting of three concentric black, white, and gray rings (Fig. 1, top panel). The radial background moved continuously in an inward direction (small white arrows) during the entire duration of the imaging run. In RADIAL, the face remained static, and the radial background either moved in the direction indicated by the white arrows or remained static. The effect of an inwardly moving radial background was generated by changing the color of the concentric rings on each frame (see bottom panel). The bottom panel depicts a schematic of a single cycle in the ABAB alternating design for the EYES versus MOUTH task. The duration of each subtask (A or B) was 6 sec. During each subtask, a series of 10 images (600 msec duration) was shown. In subtask A, the eyes shifted their position from the center to either left or right and back to center in a random manner. In subtask B, the mouth closed on alternate frames.

Figure 1. The top panel illustrates the six experimental tasks. In EYES, lateral eye movements were contrasted to a static face with the eyes looking straight ahead. In MOUTH, an open mouth was contrasted to a closed mouth in a static face. Eye movements were contrasted with mouth movements in the EYES versus MOUTH task. In SIMULATED (SIM) EYES and SIMULATED MOUTH, colored checkerboard patterns with checks reversing position in spatially equivalent positions (white arrows) to the real eyes and mouth were contrasted to a static checkerboard. In all of these tasks the radial background moved continuously in an inward direction (small white arrows) during the entire duration of the imaging run. In RADIAL, the face remained static, and the radial background either moved in the direction indicated by the white arrows or remained static. The effect of an inwardly moving radial background was generated by changing the color of the concentric rings on each frame (see bottom panel). The bottom panel depicts a schematic of a single cycle in the ABAB alternating design for the EYES versus MOUTH task. The duration of each subtask (A or B) was 6 sec. During each subtask, a series of 10 images (600 msec duration) was shown. In subtask A, the eyes shifted their position from the center to either left or right and back to center in a random manner. In subtask B, the mouth closed on alternate frames.
center. Thus, the subject viewed alternating periods of eye movements and fixation on an otherwise stationary face. The purpose of this manipulation was to identify brain regions activated by movement of the eyes.

During both subtasks of EYES, the radial background seemed to continuously move inward. This radial motion was designed to activate brain regions sensitive to motion per se and to diminish their contribution to the activation differences between eye movement and eye fixation.

The MOUTH task was similar to the EYES task. In subtask A, the mouth within the face seemed to open and close. In subtask B, the mouth remained closed. The radial background moved continuously in both subtasks, as described above. The purpose of this task was to identify brain regions activated by mouth movements.

In the EYES versus MOUTH task (Fig. 1, bottom panel), subtask A consisted of moving eyes as described above for EYES. Subtask B consisted of the moving mouth as described above for MOUTH. Thus, in this task the subject viewed alternating periods of eye and mouth movements. This task was designed to identify activations specific to eye or mouth movement while de-emphasizing activations common to both types of movement. The radial background continuously moved inward as described above.

In the SIMULATED EYES task, the face was replaced by an oval equal in area to the average area of the two faces used in the previous tasks. The oval contained a rectangular dynamic display. The overall luminance and contrast of which were equal to the average luminance and contrast of the two individual faces. The check colors were chosen from the red–green–blue values of the faces and their inner components. The exposed area of the continuously moving radial background was the same as in the previous tasks. In subtask A, checks similarly located within the rectangle as the eyes were located within the face made discrete horizontal movements. The identical timing of the movements to the eye movements as described above. The movements, however, were not conjugate to avoid the illusion that the flesh-colored pattern was an abstract face. In subtask B, the checks did not move. This task was designed to determine whether activations generated by the moving eyes in the EYES and EYES versus MOUTH tasks were simply because of movement of the dynamic part of the face or whether there was an abstract physiological involvement of the eyes.

In the SIMULATED MOUTH task, subtask A consisted of the movement of checks similarly located within the rectangle as the mouth was located within the face and equal in area. The movement of the checks mimicked the opening and closing movements of the mouth. No movements occurred in subtask B. The radial background moved continuously during both subtasks A and B.

In the RADIAL task, a stationary face was presented during the entire imaging run. In subtask A, the radial background moved inward as described above. However, in subtask B the radial background did not move. This task was designed to identify brain areas activated by the radial motion.

Subjects were instructed to attend to the stimulus on the screen and to focus on a point midway between the eyes of the face for the duration of each run. Immediately before the first run, subjects were taught to close their eyes. The instructions were repeated just before the next run. In all imaging runs, subjects were instructed to focus on a point on the front of the headboard. The instructions emphasized that if eye movements occurred, the probability of a voxel with purely random variation having a mean t value > 1.96 is 0.00125 (or 0.0025 when tested two-tailed). Activated voxels were then superimposed on higher-resolution anatomical images for each subject as the basis of analysis. Because the scaling involved with image interpolation can smooth the shape of the activation, all quantitative analyses were performed on uninterpolated activation images. The Talairach coordinates (Talairach and Tournoux, 1988) of activated voxels were then determined. Finally, the anatomical locations of activated voxels were determined by two investigators working together and were classified using the atlas of Duvernoy (1991). The activated voxels within each anatomical structure were then counted and further categorized as described below.

The functional images of the first run per subject were averaged over the four anatomical groups based on contiguity and previous functional findings (Fig. 2). The dorsomedial region included the cingulate, superior parietal, superior occipital, angular, and supramarginal gyr, the intraparietal and cingulate sulci, and the precuneus. The lateral region included the superior temporal, middle temporal, inferior temporal, and middle occipital gyri, the Sylvian, superior temporal, inferior temporal, and lateral occipital sulci, and the parieto-temporo-occipital fossa (PTOF) (Vaina, 1994). The PTOF and nearby cortex is a movement-sensitive region (Watson et al., 1993; McCarthy et al., 1995; Tootell et al., 1995) probably homologous to monkey movement-sensitive areas MT/V5 and MST (Maunsell and Van Essen, 1983; Desimone and Ungerleider, 1986; Tanaka and Saito, 1989; Lagae et al., 1994). We will use the term PTOF to refer to an anatomically defined region and the term MT/V5 for functionally defined movement-sensitive cortex. The ventral region comprised the fusiform, inferior occipital and fourth occipital gyri, and the occipitotemporal and inferior occipital sulci. The ventral region includes those regions strongly activated by faces in previous functional magnetic resonance imaging (fMRI) studies (Puce et al., 1995, 1996; Clark et al., 1996; Kanwisher et al., 1997; McCarthy et al., 1997). The ventromedial region included the collateral and calcarine sulci, the lingual and cuneate gyri, and the cuneus and parieto-occipital fissure. Within subjects, repeated ANOVAs were computed in which the number of activated voxels was the dependent variable and the task, hemisphere (left or right), slice (1–7), and anatomical region (lateral, dorsomedial, ventromedial, and ventral) were independent variables.
EYES, SIMULATED MOUTH, or RADIAL. In contrast, all 1 and 2 for EYES and MOUTH but not for SIMULATED 
stimulation of the right STS to EYES was observed in coronal slices 1–3 and RADIAL from coronal and axial imaging sessions. Activa-
with additional bilateral activation of the PTOF in slice 5. Similar 
temporal sulcus;
MTG 

Figure 2.

Figure 2. Four anatomical regions for classification of activated voxels (lateral, dorsomedial, ventromedial, and ventral) and their borders are outlined on the left side of a coronal anatomical image. Some of the structures falling within each region are shown on the right. STS, Superior
temporal sulcus; MTG, middle temporal gyrus; ITS, inferior temporal sulcus; ITG, inferior temporal gyrus; OTS, occipitotemporal sulcus; FG, fusiform gyrus; CS, collateral sulcus; LG, lingual gyrus; CaS, calcarine 
sulcus; POF, parieto-occipital fissure; PrC, precuneus; Ct, cingulate gyrus 
and sulcus; SPG, superior parietal gyrus; ITS, intraparietal sulcus; AG/ 
SuG, angular or supramarginal gyr.

Four task comparisons were computed: (1) EYES, MOUTH, and RA-
DIAL; (2) EYES, MOUTH, SIMULATED EYES, and SIMULATED 
MOUTH; (3) RADIAL, SIMULATED EYES, and SIMULATED 
MOUTH; and (4) the moving eyes and moving mouth subtasks from the 
EYES versus MOUTH task. Additional analyses were performed to look 
for anatomical patterns within the structures constituting the four ana-
atomical regions.

RESULTS

Figure 3 presents results from a single subject for five experimen-
tal tasks. Five contiguous anatomical slices are shown, with the 
most anterior slice at the left. Discrete foci of activation (framed 
by white squares) in the right STS were observed in anterior slices 
1 and 2 for EYES and MOUTH but not for SIMULATED 
EYES, SIMULATED MOUTH, or RADIAL. In contrast, all 
tasks activated the right PTOF in slice 4 (framed by white circles) 
with additional bilateral activation of the PTOF in slice 5. Similar 
patterns of activation were observed in the other subjects.

Figure 4 presents results from another individual for EYES 
and RADIAL from coronal and axial imaging sessions. Activation 
of the right STS to EYES was observed in coronal slices 1–3 
(Fig. 4A, white squares) and in the corresponding regions in axial 
slices 5 and 7 (Fig. 4B, white squares). Less extensive activation of 
the left STS was also observed (Fig. 4, A, slice 2, B, slice 7, white 
quares). There was little or no activation to RADIAL in the STS 
in these slices. In contrast, activation common to both tasks was 
seen in the PTOF and the lateral occipital sulcus (LOS) (Fig. 4, 
A, coronal slices 4–7, corresponding regions in B, axial slices 
1–4).

Activation was observed in the intraparietal sulcus (IPS) to 
EYES (Fig. 4A, slices 1, 2, framed by white circles) and to 
RADIAL (Fig. 4A, slices 6, 7, framed by white circles). Activation 
was also observed in the calcarine cortex and collateral sulcus to 
RADIAL (Fig. 4, A, slices 4–7, B, slice 1).

Activation in the lateral region

Consistent with the illustrative data of Figures 3 and 4, the 
greatest number of activated voxels occurred within the lateral 
region for all conditions in all subjects. EYES and MOUTH 
produced activation mainly in the anterior slices (Fig. 5, top), 
whereas RADIAL produced activation mainly in slices 4 and 5 of 
the left hemisphere (p < 0.01 for task; p < 0.05 for slice; p < 0.01 
for hemisphere × task × slice).

When the number of activated voxels in the right lateral region 
was examined as a function of anatomical structure, the combined 
STS and ITS accounted for 49 and 46% of the total activation for 
EYES and MOUTH, respectively (Fig. 6, left panel). The number 
of activated voxels for EYES was greater than that for MOUTH, 
but this difference did not reach statistical significance (p = 0.12).
In contrast to the activation in STS and ITS by EYES and 
MOUTH, RADIAL mainly activated the left PTOF and the 
LOS (Fig. 6, right panel), which together accounted for 58% of 
the total activation across all slices in left lateral cortex.

As illustrated in Figures 3 and 4, the activation in lateral cortex 
formed two discontinuous clusters, an anterior cluster elicited 
mainly by EYES and MOUTH and a posterior cluster elicited by 
all three tasks. The centroids of these clusters were calculated for 
EYES, MOUTH, and RADIAL. The anterior centroids were 
calculated in two ways: (1) an unrestricted method that included 
all activated voxels from the Sylvian fissure to the inferior 
temporal gyrus regardless of their proximity to the major activation 
cluster; and (2) a restricted method that included only activated 
voxels from the STS and ITS, in which the major activation 
occurred. A similar approach was used to calculate the posterior 
centroids. The unrestricted calculation included voxels from the 
PTOF, LOS, and middle occipital gyrus, whereas the restricted 
calculation included only voxels from the PTOF and LOS. As 
shown in Table 1, the centroids for the unrestricted and restricted 
calculations were virtually identical. Thus, the centroids 
calculated 
from the more restricted anatomical structures provide an 
accurate representation of the results. A graphical depiction of 
these centroids is shown superimposed on a sagittal view of a 
representative brain in Figure 7, in which the close spatial corre-
spondence of the anterior centroids for EYES and MOUTH can 
be appreciated. The spatial overlap of the posterior centroids for 
EYES, MOUTH, and RADIAL is also apparent.

The preferential activation of STS to EYES and MOUTH is 
shown in Figure 8. Here, a single cycle of activation was created 
by averaging across all cycles for each of the EYES and MOUTH 
tasks for 10 subjects (one subject with no activation to any task 
was eliminated). The activated voxels in the right STS were 
interrogated across the image time series for all experimental 
runs. The magnetic resonance activation signal in the right STS 
(Fig. 8) increased steadily during eye or mouth movement and 
then decayed after movement cessation. The peak signal change 
was 0.7%. There was negligible activation in these same voxels by 
RADIAL.

Fewer voxels were activated within the lateral region during the 
EYES versus MOUTH task. Only 40% of the voxels activated in 
EYES were activated by moving eyes within EYES versus 
MOUTH. Moving mouths within EYES versus MOUTH pro-
duced 67% of the voxels activated by MOUTH. These results 
suggest considerable overlap in the activation by EYES and 
MOUTH. The statistical analysis for EYES versus MOUTH 
(Fig. 5, slices 1, 2) showed only a significant main effect of slice 
(p < 0.01), indicating that activation occurred primarily in ante-
rior slices.

Even fewer voxels were activated in SIMULATED EYES and 
SIMULATED MOUTH tasks. Significantly fewer voxels were 
activated when both control tasks were compared with EYES and
MOUTH (task $p < 0.01$) or with RADIAL (task, $p < 0.01$). No other significant effects or interactions were noted. The restricted posterior activation centroids for the SIMULATED EYES and SIMULATED MOUTH were similar to those of EYES, MOUTH, and RADIAL (Table 1).

The results of the 11 subjects tested with coronal slices showed that the most consistent activation to EYES and MOUTH occurred in the most anterior slices. This raised the concern that our coronal slices may have been posterior to the main locus of activation. For this reason, the six subjects with the strongest activation in the lateral region were rescanned in an oblique axial-imaging study for the EYES, MOUTH, and RADIAL tasks. The patterns of activation in the axial study were similar to those in the coronal study for both hemispheres (Fig. 7, Table 1), indicating that the coronal study encompassed the main locus of activation to EYES and MOUTH. The posterior activation centroids in the axial study were virtually unchanged from the coronal study (Fig. 7, Table 1).

**Activation in the dorsomedial region**

Fewer voxels were activated within the dorsomedial region than the lateral region. The most prominent activation occurred for EYES in slices 1 and 2 of the left hemisphere (Figs. 4A, slices 1, 2, white circles, 5, second from top) and for RADIAL in slices 5–7 in both hemispheres (Figs. 4B, slices 6, 7, white circles, 5, second from top). These observations were confirmed by ANOVA, which revealed a significant main effect of task ($p < 0.05$) and a significant interaction effect of hemisphere $\times$ task $\times$ slice ($p <$
The IPS contributed 59, 45, and 70% of the activated voxels in EYES, MOUTH, and RADIAL, respectively. EYES preferentially activated the left anterior IPS, whereas RADIAL activated the posterior IPS in both hemispheres (Fig. 4, white circles).

Statistical comparison of the EYES versus MOUTH task revealed only a main effect for slice ($p < 0.05$), confirming that more activation occurred in the anterior slices. Greater activation occurred to EYES and MOUTH than to SIMULATED EYES and SIMULATED MOUTH in the anterior slices ($p < 0.05$; slice, $p < 0.01$; hemisphere × task × slice, $p < 0.05$). A comparison of RADIAL, SIMULATED EYES, and SIMULATED MOUTH revealed greater activation to RADIAL ($p < 0.01$; hemisphere × task × slice, $p < 0.01$).

Activation in the ventromedial region

Strong posterior activation occurred in slices 4–7 for the RADIAL task ($slice, p < 0.01; task, p < 0.01$), whereas EYES and MOUTH elicited negligible activation (Fig. 5, second from bottom). The collateral sulcus and the lingual gyrus combined produced 81% of the activation in this region.

Activation in the ventral region

The ventral region produced the fewest number of activated voxels of the four regions, with the greatest concentration occurring in slices 3–5 ($slice, p < 0.05$) but with no significant differences among RADIAL, EYES, and MOUTH (Fig. 5, bottom).

DISCUSSION

The major results of this study indicate that a region of the temporal lobe centered in the STS is activated when subjects view a face in which the eyes or mouth are moving (Figs. 7, 8). The active region comprises the posterior portion of the straight segment of the STS (Fig. 7). These activations were not attributable to movement per se. Nonfacial movement in the same part of...
Figure 5. Voxel counts as a function of hemisphere (R, right; L, left) and slice for each region in 11 subjects. Lateral (top), dorsomedial (second from top), ventromedial (second from bottom), and ventral (bottom) for EYES (gray histograms), MOUTH (white histograms) and RADIAL (black histograms). Slice 1 is the most anterior, and slice 7 is the most posterior. EYES elicited more activation in slices 1–3 than the other two tasks, whereas RADIAL elicited the most prominent activation in slices 4–7 in the left hemisphere. In the dorsomedial region, the most prominent activation was elicited to EYES in slices 1 and 2 of the left hemisphere and to RADIAL in slices 5–7 of both hemispheres. In the ventromedial region, RADIAL elicited the most prominent activation in slices 4–7 of both hemispheres. The least activation was seen in the ventral region and was not different across tasks.
Figure 6. Voxel counts as a function of hemisphere and anatomical structure for the lateral region for EYES (gray histograms), MOUTH (white histograms), and RADIAL (black histograms) in 11 subjects. In the right hemisphere, EYES produced the most activation in the STS, whereas in the left hemisphere the most activation occurred in the PTOF and LOS to radial. Syl, Sylvian fissure; STG, superior temporal gyrus; STS, superior temporal sulcus; MTG, middle temporal gyrus; ITS, inferior temporal sulcus; ITG, inferior temporal gyrus; PTOF, parieto-temporo-occipital fossa; LOS, lateral occipital sulcus; MOG, middle occipital gyrus.

Table 1. Activation centroids in Talairach coordinates ($x$, $y$, $z$) and SEM

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<td>-49</td>
<td>1</td>
</tr>
<tr>
<td>Mouths</td>
<td>45</td>
<td>6</td>
<td>-57</td>
<td>6</td>
<td>7</td>
<td>4</td>
<td>-48</td>
<td>2</td>
</tr>
<tr>
<td>PTOF + LOS</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eyes</td>
<td>39</td>
<td>6</td>
<td>-72</td>
<td>7</td>
<td>-1</td>
<td>3</td>
<td>-40</td>
<td>8</td>
</tr>
<tr>
<td>Mouth</td>
<td>36</td>
<td>4</td>
<td>-71</td>
<td>5</td>
<td>-1</td>
<td>2</td>
<td>-37</td>
<td>8</td>
</tr>
<tr>
<td>Radial</td>
<td>43</td>
<td>3</td>
<td>-69</td>
<td>3</td>
<td>-5</td>
<td>4</td>
<td>-33</td>
<td>1</td>
</tr>
</tbody>
</table>

Anterior lateral cortex and posterior lateral cortex refer to unrestricted activation centroids, whereas STS + ITS and PTOF + LOS refer to restricted activation centroids.
the visual field as occupied by the eyes or mouth, or movement of a radial background, activated an area that was ventral and posterior to this region (the PTOF and LOS), corresponding to area MT/V5. As can be seen in Figure 9, the activation centroids in MT/V5 in the present study correspond closely to those reported in other studies of nonbiological motion.

These results suggest that a discrete region of cortex centered in the STS is involved in the perception of eye and mouth movement. That such regions may be lateralized is suggested by Campbell et al. (1986), who reported that a prosopagnosic patient with a right occipitotemporal lesion was deficient in determining direction of gaze but could lip-read normally, whereas a patient with a left occipitotemporal lesion was alexic and could not lip-read but could recognize familiar faces and determine direction of gaze normally. We found that changes in direction of gaze activated the right STS more than the left. However, this difference did not reach statistical significance ($p = 0.10$). Calvert et al. (1997) reported that silent lip-reading of words activated a bilateral region of the superior temporal gyrus (presumably including cortex within the STS) 2.2–3.0 cm anterior to the bilateral regions described here (Fig. 9). The STS may also participate in the perception of biological motion. When subjects viewed point-light simulations of hand action, body movement, object motion, and random motion, a region of the STS was activated by hand and body movement but not by the other movement tasks (Bonda et al., 1996). Their activations were 0.5–1.5 cm posterior and superior to the region activated in our study (Fig. 9). In positron emission tomographic studies, Rizzolatti et al. (1996) found that the observation of grasping movements activated the left middle temporal gyrus and STS centered at $y = -21$ (Grafton et al., 1996). This region is considerably anterior (Fig. 9) to the region activated by hand...
action by Bonda et al. (1996) for reasons that are unclear. However, taken together these studies strongly implicate the human STS and adjacent cortex in the perception of facial and body movements of other individuals.

In previous fMRI studies, we reported two regions activated by faces (Puce et al., 1995, 1996). The major activation occurred in ventral occipitotemporal cortex, primarily within the fusiform gyrus. It is notable that this region showed negligible activation in the present study, presumably because of the continuous presence of a face during each task. We also reported activation of lateral cortex by faces, including activation within the PTOF and in and near the STS (Fig. 9) (Puce et al., 1995, their Fig. 7). The activation of these same regions in the present study by moving eyes and mouths suggests a functional dissociation between the ventral and lateral regions activated by faces.

Further support for a functional dissociation in face processing is derived from differences we have observed between intracranial and scalp ERP recordings. An intracranial ERP (N200), recorded primarily from the fusiform gyrus (Allison et al., 1994a,c), is evoked predominantly by faces and to a lesser extent by nonface stimuli. N200 is larger to faces than to eyes and other face parts viewed in isolation (Allison et al., 1994b). A similar face-specific ERP (N170) can be recorded from the lateral temporal scalp. N170 is larger to eyes viewed in isolation than to faces, leading Bentin et al. (1996) to conclude that N170 reflects activity in a different eye-sensitive region of cortex. The neural generator of the scalp-recorded N170; hence, the location of the eye-sensitive region is unknown. Bentin et al. (1996) concluded on the basis of its location and orientation that the fusiform gyrus was an unlikely generator of N170 and instead proposed the occipitotemporal sulcus (OTS). The present study shows that moving eyes primarily activate the STS and not the OTS. The STS and adjacent surface cortex is favorably located for the generation of N170, but this issue is unresolved and complicated by the fact that Bentin et al. (1996) used static views of faces and isolated eyes. It may be that eye movement is necessary to engage the STS. However, combined with the present study, these results suggest that there are two separate systems participating in the processing of information relating to faces: a ventral region involved with faces and a lateral region concerned with face com-

Figure 9. Centroids of activation (STS/ITS for EYES and MOUTH and PTOF/LOS for RADIAL) in this study compared with centroids of activation for the perception of hand action or body movement (Bonda et al., 1996), hand grasping (Rizzolatti et al., 1996; Grafton et al., 1996), silent lip-reading of numbers (Calvert et al., 1997), nonanimate movement (Watson et al., 1993; McCarthy et al., 1995; Tootell et al., 1995), and the perception of static faces (Puce et al., 1995, 1996). A, Right hemisphere. B, Left hemisphere. Centroids of activation are superimposed on two sagittal views of a representative brain.
ponents, or the movement of face components. The former system would provide information necessary for the recognition of facial identity, whereas the latter would provide information necessary for the successful interpretation of facial gesture.

Direction of gaze is thought to be an important facial gesture. In monkeys, gaze direction is an important component of facial expressions, particularly those related to dominance and submission (Hinde and Rowell, 1962; Mendelson et al., 1982; Perrett et al., 1990; Perrett and Mistlin, 1990; Brothers and Ring, 1993). Given the importance of these facial signals, it is not surprising that some neurons in monkey temporal visual cortex (primarily in the STS) are sensitive to eye and head direction (Hasselmo et al., 1989; Perrett et al., 1985, 1992). These neurons may play a role in what Perrett et al. (1992) call “social attention,” or cells that signal the direction of another individual’s attention. In the monkey temporal lobe, cells responsive to direction of gaze tend to be located within the STS, whereas cells responsive to face identity tend to be located in adjacent inferior temporal cortex (Yamane et al., 1988; Hasselmo et al., 1989; Perrett et al., 1990, 1992). In humans and monkeys, direction of gaze provides information in social situations, expresses intimacy, and allows inferences about the direction of attention of another individual (Kleinke 1986; Perrett and Mistlin, 1990). We suggest that the superior temporal region activated by moving eyes (Fig. 9) is involved in the perception of direction of gaze.

This same region of superior temporal cortex also responded to mouth movement (Fig. 9). In monkeys, mouth movements are also an important component of facial gesture. For example, mouth opening and teeth baring are components of threat or fear for many species, whereas “smiling” denotes submission or a positive affect (Chevalier-Skolnikoff, 1973; Redican, 1982). It is possible that in humans the STS and surrounding cortex are involved in the interpretation of facial gestures involving the mouth. We have interpreted our results to mean that the activated portion of the STS is preferentially involved in the perception of dynamic facial movement. Although plausible, this interpretation remains unproven, because (1) we have not studied activation evoked by eye and mouth movement compared with static views of direction of gaze or mouth configuration; (2) we have not studied the possible activation of this region by complex but inanimate objects, e.g., a swinging pendulum; and (3) the responsiveness of monkey STS cells to moving eyes and mouths has not yet been reported.

Aside from the activations already discussed, the only other substantial activation occurred bilaterally in the IPS. The IPS is a large structure and likely functionally diverse. For example, it is activated by viewing gratings (Gulyás and Roland, 1995), by viewing letter strings and faces (Puce et al., 1996), and by reading music (Sergent et al., 1992b). The functional significance of IPS activation in this study is unknown. However, the radial task primarily activated the posterior portion of the IPS, suggesting that this region may be a component of the dorsal visual pathway dealing with movement and spatial location.

Finally, we note that EYES activated area MT/V5 in the right hemisphere only slightly less than did RADIAL (Fig. 6), although the radial background moved continuously during the EYES task. Thus, the continuously moving radial background did not control movement per se in the EYES task in MT/V5. We consider four possible explanations. First, EYES may have activated a population of MT/V5 cells responsive to more central portions of the visual field, in addition to the cells responsive to the peripheral radial background. This explanation does not, however, account for the relative lack of MT/V5 activation by MOUTH, SIMULATED EYES, and SIMULATED MOUTH, which also included movements in the central portions of the visual field. Second, MT/V5 may be more sensitive to coherent motion, such as that produced by conjugate eye movements, than by the noncoherent motion of the other tasks. Third, activation of MT/V5 above that elicited by the moving radial background may represent attentional modulation (O’Craven et al., 1997). Moving eyes may be a highly salient stimulus and thus may engage attention more than the other tasks. Last, MT/V5, or a subregion of it, may in fact be sensitive to moving eyes. Single-unit recordings in monkey MT/MST have determined its responsiveness to moving slits, dots, optical flow, and other kinds of nonbiological movement (Maunsell and Van Essen, 1983; Desimone and Ungerleider, 1986; Tanaka and Saito, 1989; Lagae et al., 1994). A portion of STS receives input from MST (Baizer et al., 1991). If the human STS has a similar connectivity, the region of STS described here may receive input from a region of MT/V5 that itself is responsive to eye movement. Whether a population of cells preferentially responsive to movements of animate objects is present in monkey MT/MST, and whether such results could explain the activation of MT/V5 by eye movements in this study, remain to be determined.

REFERENCES

Gulyás B, Roland PE (1995) Cortical fields participating in spatial fre-


