# Visual Imagery of Famous Faces: Effects of Memory and Attention Revealed by fMRI

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**Complex pictorial information can be represented and retrieved from memory as mental visual images. Functional brain imaging studies have shown that visual perception and visual imagery share common neural substrates. The type of memory (short- or long-term) that mediates the generation of mental images, however, has not been addressed previously. The purpose of this study was to investigate the neural correlates underlying imagery generated from short- and long-term memory (STM and LTM). We used famous faces to localize the visual response during perception and to compare the responses during visual imagery generated from STM (subjects memorized specific pictures of celebrities before the imagery task) and imagery from LTM (subjects imagined famous faces without seeing specific pictures during the experimental session). We found that visual perception of famous faces activated the inferior occipital gyri, lateral fusiform gyri, the superior temporal sulcus, and the amygdala. Small subsets of these face-selective regions were activated during imagery. Additionally, visual imagery of famous faces activated a network of regions composed of bilateral calcarine, hippocampus, precuneus, intraparietal sulcus (IPS), and the inferior frontal gyrus (IFG). In all these regions, imagery generated from STM evoked more activation than imagery from LTM. Regardless of memory type, focusing attention on features of the imagined faces (e.g., eyes, lips, or nose) resulted in increased activation in the right IPS and right IFG. Our results suggest differential effects of memory and attention during the generation and maintenance of mental images of faces.**

***Key Words:* face perception; functional MRI; visual imagery.**

## INTRODUCTION

When recalling visual information, we often see pictures in our "mind's eye." The ability to generate visual images in the absence of any retinal input is a vivid demonstration of memory and cognition in operation. Brain imaging and psychophysical studies have demonstrated functional similarities between visual perception and visual imagery, to the extent that common cortical regions and mechanisms appear to be activated by both (Roland *et al.,* 1987; Farah *et al.,* 1988; Goldenberg *et al.,* 1989; Ishai and Sagi, 1995, 1997a,b). Numerous neuroimaging studies have shown that visual imagery, like visual perception, evokes activation in occipitoparietal and occipitotemporal visual association areas (Roland and Gulyas, 1995; Mellet *et al.,* 1995, 1996; D'Esposito *et al.,* 1997). In some studies, the primary visual cortex (Le Bihan *et al.,* 1993; Kosslyn *et al.,* 1993, 1995, 1996, 1999; Klein *et al.,* 2000; Thompson *et al.,* 2001; Lambert *et al.,* 2002) and the lateral geniculate nucleus (Chen *et al.,* 1998) were activated during visual imagery, suggesting that the generation of mental images may involve sensory representations at the earlier processing stages in the visual pathway. Recent fMRI studies have reported category-related activation in ventral temporal cortex during visual imagery of faces and other objects, suggesting that content-specific memory traces are localized in these higher visual areas (Ishai *et al.,* 2000a; O'Craven and Kanwisher, 2000).

The purpose of this study was to investigate the neural mechanisms underlying visual imagery generated from short-term memory (STM) and from long-term memory (LTM). Behavioral studies have reported differential effects of visual imagery on the performance of a perceptual task: While visual recall from STM facilitated task performance, visual recall from LTM interfered with performance, indicating that imagery-induced facilitation and interference are memory-dependent (Ishai and Sagi, 1995, 1997a,b). Moreover, the type of memory (short- or long-term) required for the generation of mental images seems to be a crucial factor in the V1 debate. In the vast majority of studies reporting activation in the calcarine, the imagery tasks were based on recall from STM (e.g., Le Bihan *et al.,* 1993; Kosslyn *et al.,* 1993, 1995, 1996, 1999; Chen *et al.,* 1998; Goebel *et al.,* 1998; O'Craven and Kanwisher, 2000; Thompson *et al.,* 2001). For example, prior to a letter imagery task, subjects were visually presented with those letters (Kosslyn *et al.,* 1993), suggesting that maintaining a trace in a short-term buffer is required for activation in V1. On the other hand, imagery tasks that required the generation of images from LTM have not found activation in V1 (Roland *et al.,* 1987; Roland and Gulyas, 1995; Mellet *et al.,* 1995, 1996, 1998, 2000a,b; D'Esposito *et al.,* 1997; Ishai *et al.,* 2000a; Knauff *et al.,* 2000; Gulyas, 2001), with the exception of a recent event-related fMRI study (Klein *et al.,* 2000). To our knowledge, previous neuroimaging studies have

not addressed the question of memory type (STM or LTM) required for the generation of visual images. We thus decided to compare, within the same subject and the same experimental session, whether similar or different cortical regions are activated during visual imagery generated from STM and from LTM. To that end, we had to use a special class of stimuli. We chose faces of contemporary celebrities, assuming that as a result of exposure to those faces in everyday life, subjects would have pictorial representations in memory that could be retrieved by way of visual imagery. Moreover, giving the same visual cue, that is, a famous name, an image could be generated from either LTM or STM. For example, one can imagine Marilyn Monroe without seeing her picture before the imagery task (LTM) or one can memorize a specific picture of Marilyn Monroe and then generate a mental image of that picture (STM).

We were also interested in the effect of focal attention during visual imagery. Functional brain imaging studies have shown that selective attention to particular attributes of visual stimuli enhanced the activity in regions of extrastriate cortex that process these attributes. For example, selective attention to shape and color increased the response in the fusiform gyrus (Corbetta et al., 1990; Clark et al., 1997), while selective attention to speed and motion enhanced the activity in area MT (Corbetta et al., 1990; Beauchamp et al., 1997). Motivated by the functional similarities between perception and imagery, we hypothesized that focusing attention on features of a mental image, rather than on the global configuration of that image, might also result in increased activation. Moreover, according to the model suggested by Sakai and Miyashita (1994), visual imagery is implemented by the interactions between memory retrieval of representations stored in higher visual association areas and the effect of focal attention on early visual areas. Accordingly, we speculated that focal attention to mental images would evoke activation in the calcarine. To test these attention predictions, our experimental design included imagery conditions in which subjects had to answer questions about the faces they imagined (e.g., "big nose?"). We reasoned that to answer the questions, subjects would have to focus their attention on the relevant facial features and thus hypothesized that this focal attention would result in differential patterns of brain activity.

As we and others have previously shown, face perception is mediated by a distributed neural system in the human brain that consists of "core" and "extended" systems (Haxby et al., 2000). The "core" system is composed of regions in the visual cortex, that is, the inferior occipital, fusiform gyri, and superior temporal sulcus (STS), which mediate the visual analysis of faces. The ventral regions in this core system participate more in the recognition of individuals (Kanwisher et al., 1997; McCarthy et al., 1997; Gauthier et al., 1999; Haxby et al., 1999; Ishai et al., 1999, 2000b). The more dorsal regions (i.e., the STS) participate in the perception of eye gaze direction, speech-related lip movements, and expression (Puce et al., 1999; Hoffman and Haxby, 2000). The extended system includes the amygdala, which participates in the perception of the emotional content of facial expression (Breiter et al., 1996; Morris et al., 1996; Phillips et al., 1997). Previous neuroimaging studies of *familiar* faces (celebrities, personally familiar, or newly learned faces) have found activation in similar visual areas that were activated by unfamiliar faces,

most consistently in the fusiform gyrus (Sergent et al., 1992; Gorno-Tempini et al., 1998; Dubois et al., 1999; Leveroni et al., 2000; Nakamura et al., 2000; Campanella et al., 2001; Gorno-Tempini and Price, 2001; Rossion et al., 2001; Shah et al., 2001). In some reports, the direct comparison between familiar and unfamiliar faces revealed activation in an anterior middle temporal region, suggested to be the locus for the analysis of unique semantic attributes (Sergent et al., 1992; Gorno-Tempini et al., 1998; Leveroni et al., 2000; Nakamura et al., 2000; Gorno-Tempini and Price, 2001). We thus predicted that famous faces would evoke activation in the above-mentioned regions and reasoned that the localized visual response would facilitate comparison with the response evoked during visual imagery.

We report here that visual perception of famous faces activated the inferior occipital gyri, lateral fusiform gyri, the STS, and the amygdala. Visual imagery activated small subsets of these face-selective regions. Additionally, visual imagery of famous faces activated a network of regions composed of bilateral calcarine, hippocampus, precuneus, intraparietal sulcus (IPS), and the inferior frontal gyrus (IFG). In all these regions, imagery generated from STM evoked more activation than imagery from LTM. Focusing attention on features of the imagined faces resulted in increased activation in the right IPS and right IFG, during imagery generated from both STM and LTM.

## METHODS

### Subjects

Nine normal, right-handed subjects (five men, four women, age 27 ± 4 years), with normal vision, participated in this study. All subjects gave written informed consent for the procedure in accordance with protocols approved by the NIMH Institutional Review Board.

### Stimuli

Stimuli were generated by a Macintosh computer (Apple, Cupertino, CA), using SuperLab (Cedrus, Wheaton, MD; Haxby et al., 1993), and were projected with a magnetically shielded LCD video projector (Sharp, Mahwah, NJ) onto a translucent screen placed at the feet of the subject. The subject viewed the screen by a mirror system. Subjects were presented with gray-scale photographs of contemporary celebrities, phased scrambled pictures of faces (retaining spatial frequency information), or names of famous faces (see Appendix). The scrambled pictures were created by use of the Fourier transform with an in-house Matlab script. The phase information was then randomized and recombined with the picture's original magnitude information by using the inverse Fourier transform algorithm. All stimuli were presented in the center of the screen on a black background.

We chose scrambled faces as the control for the perception condition, to detect bilateral activation in multiple regions of the extended face perception network and not just the small regions that respond maximally to faces compared with common objects (Haxby et al., 1999, 2000; Ishai et al., 1999, 2000a,b).
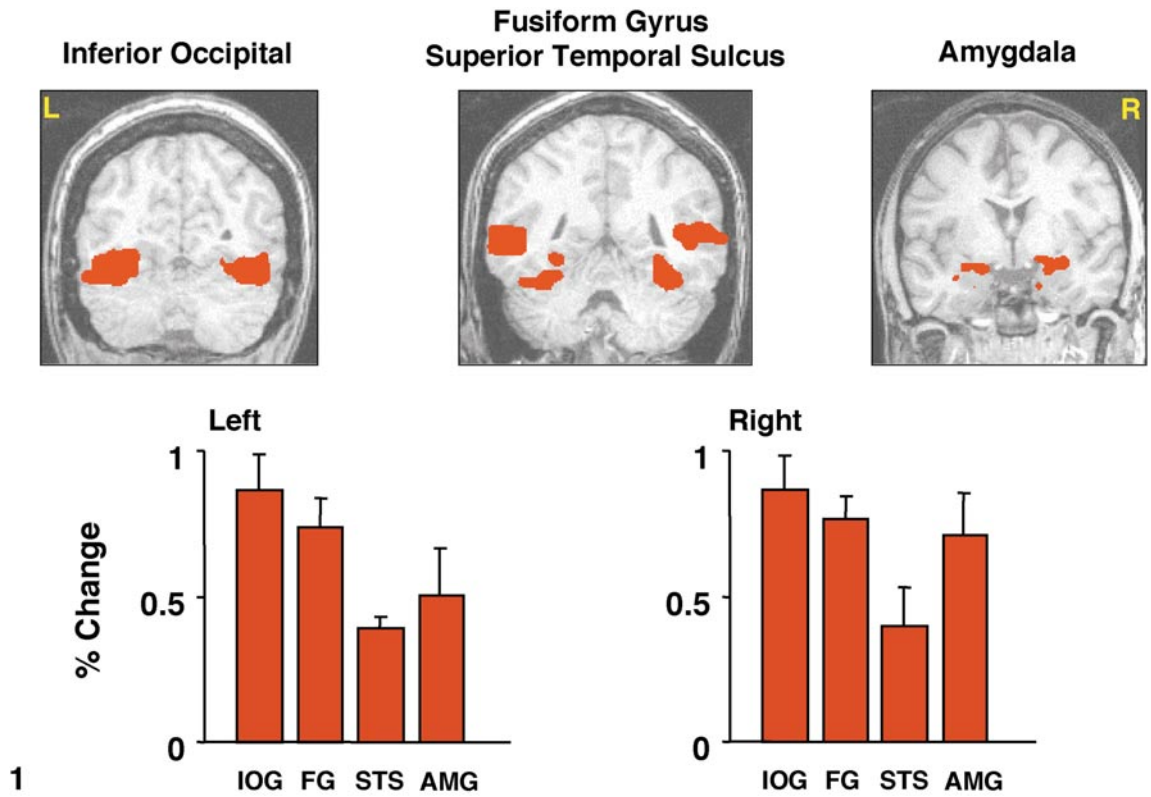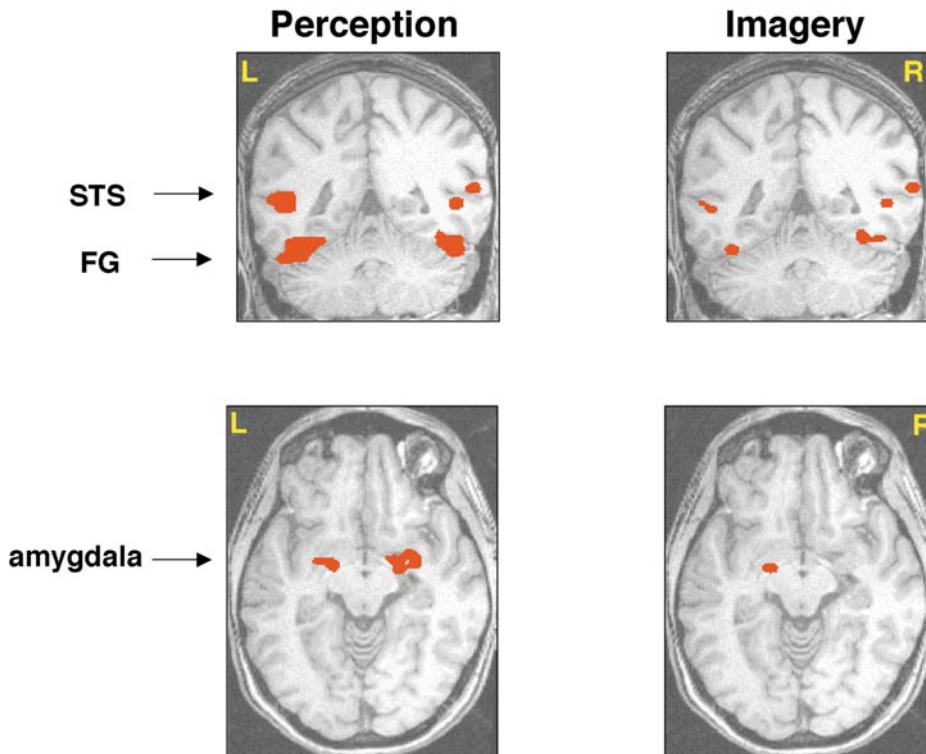
**FIG. 1.** Visual response to famous faces. (Top) Activation in the inferior occipital gyri, fusiform gyri, STS, and amygdala illustrated in coronal sections from a single subject. Voxels shown in color demonstrated a significant perception effect ($P < 0.0001$). (Bottom) Mean amplitudes of the fMRI signal in these regions. Data are averaged across all subjects and all repetitions of face presentation in each subject. Bars, SEM.

**FIG. 2.** Comparison between activation evoked by visual perception and visual imagery of famous faces, illustrated in coronal and axial sections from two subjects.

**TABLE 1**

Regions Activated during Visual Perception of Famous Faces

| Region | N | Number of voxels | X | Y | Z |
|--------|---|------------------|---|---|---|
| L IOG | 9 | 61 (10) | −36 (1) | 68 (1) | −13 (1) |
| R IOG | 9 | 77 (11) | 39 (1) | 68 (2) | −16 (1) |
| L FG | 9 | 58 (8) | −37 (2) | 47 (2) | −15 (1) |
| R FG | 9 | 62 (8) | 41 (1) | 47 (2) | −18 (1) |
| L STS | 4 | 28 (10) | −52 (1) | 34 (1) | 4 (1) |
| R STS | 6 | 24 (10) | 55 (1) | 37 (1) | 1 (2) |
| L amygdala | 7 | 17 (3) | −19 (1) | 3 (1) | −12 (1) |
| R amygdala | 9 | 17 (3) | 18 (1) | 3 (1) | −18 (2) |

*Note.* Volumes were calculated before spatial normalization. Coordinates are in the normalized space of the brain atlas of Talairach and Tournoux (1988). *N,* number of subjects in whom each region was identified. The mean for each region volume is calculated only for these subjects. Standard errors of the mean are indicated in parentheses.

*Tasks*

Subjects performed perception and imagery tasks in a standard block design. Each condition block (21 s) began with a 1-s visual cue. Each of the five runs included the following experimental conditions, and the order of condition blocks was counterbalanced across runs: (1) Perception condition, in which famous faces were presented at a rate of one per 4 s. (2) Perception control condition, during which subjects passively viewed scrambled pictures of faces, presented at a rate of one per 4 s. (3) Imagery conditions, in which subjects were presented with famous names (0.5 s) followed by a black screen (3.5 s) and were instructed to generate vivid images of these faces. The imagery conditions were:

• Imagery from STM, in which subjects were presented with names of famous faces they had seen and memorized shortly before and were instructed to generate vivid images of the exact same faces.
• Imagery from LTM, in which subjects were presented with names of famous faces they had not seen during the experiment and were instructed to generate any vivid images of these faces.
• Imagery from STM + attention (att), in which subjects were presented with names of famous faces they had seen and memorized shortly before and were instructed to generate vivid images of these faces and then answer questions about some facial feature (e.g., "thick lips?").
• Imagery from LTM + attention, in which subjects were presented with names of famous faces they had not seen

during the experiment and were instructed to generate vivid images of these faces and then answer questions about some facial feature (e.g., "big nose?").

(4) Imagery control condition, in which subjects passively viewed letter strings (0.5 s) followed by a black screen (3.5 s).

In a behavioral pilot conducted outside the MR scanner, a group of eight subjects performed the imagery tasks and were instructed to press a button after generating a vivid image of a face. The difference in reaction times (mean ± SD in milliseconds) during imagery from STM (1141 ± 472) and imagery from LTM (1059 ± 390) was not statistically significant. When subjects attended to features of the imagined faces, the reaction times were longer (STM + att, 1246 ± 408; LTM + att, 1256 ± 404). The difference, however, in reaction times between the imagery conditions that did and did not require focal attention was not statistically significant.

Before the scanning session, subjects were trained with the experimental procedure and were presented with a list of famous names (see Appendix). All subjects recognized the names and reported having representations of the corresponding faces in memory. During postscan debriefing, all subjects reported generating clear and reasonably vivid images of the famous faces.

*Data Acquisition*

A 3-T General Electric Signa scanner with a whole head coil (IGC-Medical Advances, Milwaukee, WI) was used. Changes in blood oxygen level-dependent T2*-weighted MRI

**TABLE 2**

Common Regions Activated during both Visual Perception and Visual Imagery of Famous Faces

| Region | N | Number of voxels | X | Y | Z |
|--------|---|------------------|---|---|---|
| L FG | 8 | 13 (4) | −34 (2) | 51 (1) | −14 (1) |
| R FG | 7 | 26 (10) | 38 (2) | 49 (2) | −19 (2) |
| L STS | 3 | 9 (6) | −52 (3) | 33 (5) | 3 (5) |
| R STS | 3 | 6 (3) | 54 (1) | 42 (3) | 3 (1) |
| L amygdala | 5 | 10 (3) | −18 (1) | 4 (1) | −13 (1) |
| R amygdala | 8 | 7 (2) | 17 (1) | 4 (1) | −19 (2) |

*Note.* Volumes were calculated before spatial normalization. Coordinates are in the normalized space of the brain atlas of Talairach and Tournoux (1988). *N,* number of subjects in whom each region was identified. The mean for each region volume is calculated only for these subjects. Standard errors of the mean are indicated in parentheses.

signal were measured using a gradient-echo echoplanar sequence (TR = 2 s, TE = 30 ms, FOV = 24 cm, flip angle 90°, 64 × 64 matrix). In each time series, 28 contiguous, 5-mm-thick axial slices were obtained (voxel size, 3.75 × 3.75 × 5 mm). High-resolution spoiled-gradient-recalled echo structural images were also collected (124, 1.2-mm-thick sagittal slices, TR = 15 ms, TE = 5.4 ms, FOV = 24 cm, flip angle 45°, 256 × 256 matrix). These T1-weighted images provided detailed anatomical information for registration and 3D normalization to the atlas of Talairach and Tournoux (1988).

### Data Analysis

Data were analyzed using AFNI version 2.33a (Cox, 1996; Cox and Hyde, 1997). Functional MRI scan volumes were registered to the single functional image collected closest in time to the high-resolution anatomical images (Cox and Jesmanowicz, 1999) and spatially smoothed in-plane with a 5-mm Gaussian filter.

The responses during visual perception and visual imagery of famous faces were analyzed using multiple regression (Friston *et al.,* 1995; Haxby *et al.,* 1997) with regressors related to the contrasts between famous faces versus scrambled pictures and imagery versus imagery control. Waveforms representing these effects of interest were then convolved with a canonical hemodynamic response function (Cohen, 1997).

To identify the brain regions that responded during visual perception, voxels were selected that showed a significant effect ($P < 0.0001$, uncorrected) for the contrast of famous faces versus scrambled pictures. A set of ROIs was anatomically defined for each subject, including bilaterally the inferior occipital gyri, the fusiform gyri, the STS, and the amygdala. To identify the brain regions that responded during visual imagery, voxels were selected that showed a significant effect ($P < 0.001$, uncorrected) for the contrast of imagery versus imagery control. We chose this liberal threshold because visual imagery evokes smaller responses relative to perception, in terms of both the spatial extent of the activation and the amplitude of the fMRI signal (e.g., Chen *et al.,* 1998; Goebel *et al.,* 1998; Ishai *et al.,* 2000a; O'Craven and Kanwisher, 2000). A set of ROIs was anatomically defined foreach subject, including the calcarine, hippocampus, precuneus, IPS, and IFG.

For each subject and each ROI, a mean time series, averaged across activated voxels in the region and across all runs, was calculated. These means were used for between-subjects random-effects analyses, in which the threshold for significance was set at $P < 0.05$. We also performed an ROI-based analysis on the common regions that were activated during both visual perception and visual imagery (the fusiform gyri, STS, and amygdala).

## RESULTS

### Behavioral Data

In the scanning session, subjects were instructed to press a button during two conditions: imagery from STM + attention and imagery from LTM + attention, in response to the yes/no questions (e.g., "big nose?"). The mean accuracy was 96% correct. The difference in reaction time (mean ± SD in milliseconds) between these two imagery conditions (STM + att,

1521 ± 660; LTM + att, 1447 ± 539) was not statistically significant. The longer reaction times, compared with the behavioral pilot (see Methods), likely reflects the scanner environment.

### Imaging Data

*Activation evoked by visual perception of famous faces.* Visual perception of famous faces, compared with scrambled pictures, significantly activated the inferior occipital gyri, the fusiform gyri, the STS, and the amygdala (Fig. 1). In all these visually responsive areas, we found bilateral activation (see Table 1 for cluster size and Talairach coordinates). The differences between the left and right hemispheres, in terms of both the amplitude of the response and the spatial extent of the response, were not statistically significant in the inferior occipital gyri, the fusiform gyri, and the STS. In the amygdala, the spatial extent of the activated region was larger on the right ($P < 0.05$). These findings extend our previous studies in which both passive viewing and delayed matching tasks of *unfamiliar* faces evoked activation in the inferior occipital gyri, the fusiform gyri, and the STS (Ishai *et al.,* 1999, 2000b). It is of interest that in our current study, passive viewing of famous faces, all with neutral expressions, evoked bilateral amygdalar activation in all subjects.

*Imagery effects in visually responsive areas.* Having localized the visual response evoked by famous faces, we examined the response evoked by visual imagery in these regions. We previously found that small subsets of regions in ventral temporal cortex that were activated during the perception of faces, houses, and chairs were also activated during visual imagery of these object categories (Ishai *et al.,* 2000a). Similarly, in the present study we found that in the fusiform gyri, the STS, and the amygdala, visual imagery of famous faces evoked activation in small subsets of the regions activated during visual perception (Fig. 2). The size of activated cortex and the Talairach coordinates for these regions are shown in Table 2.

We then compared the amplitude of the imagery response within the common regions that were activated during both visual perception and visual imagery (i.e., the fusiform, the STS, and the amygdala) during the four different imagery conditions. As Fig. 3 shows, imagery of famous faces generated from STM (subjects had seen and memorized the faces shortly before the imagery task) evoked more activation than imagery from LTM (subjects had not seen the faces prior to the imagery task). The difference between the amplitudes of the response during imagery from STM and imagery from LTM in each of these regions was statistically significant ($P < 0.01$; in each region data were pooled from both hemispheres).

Contrary to our prediction, we did not find differential effects of focal attention during imagery (i.e., when subjects had to answer questions about some features of the imagined faces) in these regions.

Finally, we observed a hemispheric asymmetry in the fusiform gyrus, where imagery evoked stronger activation on the left ($P < 0.01$). This finding confirms our previous report of hemispheric asymmetry during imagery of faces and other objects in ventral temporal cortex (Ishai *et al.,* 2000a; see also Goldenberg *et al.,* 1989).

*Activation evoked by visual imagery of famous faces.* Based on the response during visual imagery of famous faces,
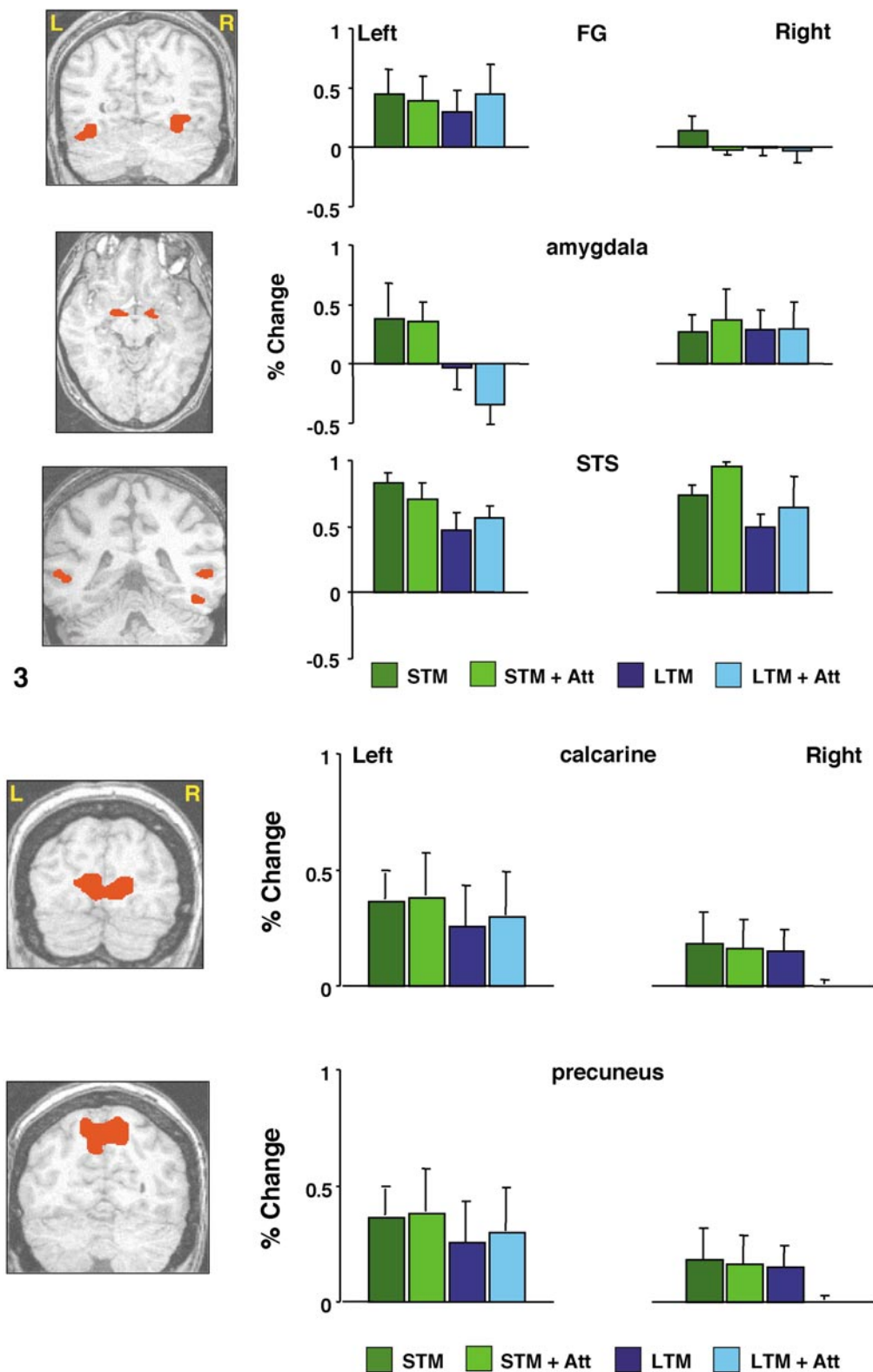
**FIG. 3.** Imagery responses in the fusiform (top), amygdala (middle), and STS (bottom). The location of activation is illustrated on the left in sections from three different subjects. The mean amplitudes of the fMRI signal in these regions are averaged across all subjects and all repetitions of task block in each subject. Bars, SEM.

**FIG. 4.** Imagery responses in the calcarine and precuneus. The location of activation is illustrated on the left in coronal sections from two different subjects. Voxels shown in color demonstrated a significant imagery effect ($P < 0.001$). The mean amplitudes of the fMRI signal in these regions are averaged across all subjects and all repetitions of task block in each subject. Data are shown for the left and right hemispheres. Bars, SEM.

**FIG. 5.** Imagery responses in the IPS and IFG. The location of activation is illustrated on the left in coronal sections from two different subjects. Voxels shown in color demonstrated a significant imagery effect ($P < 0.001$). The mean amplitudes of the fMRI signal in these regions are averaged across all subjects and all repetitions of task block in each subject. Data are shown for the left and right hemispheres. Bars, SEM.
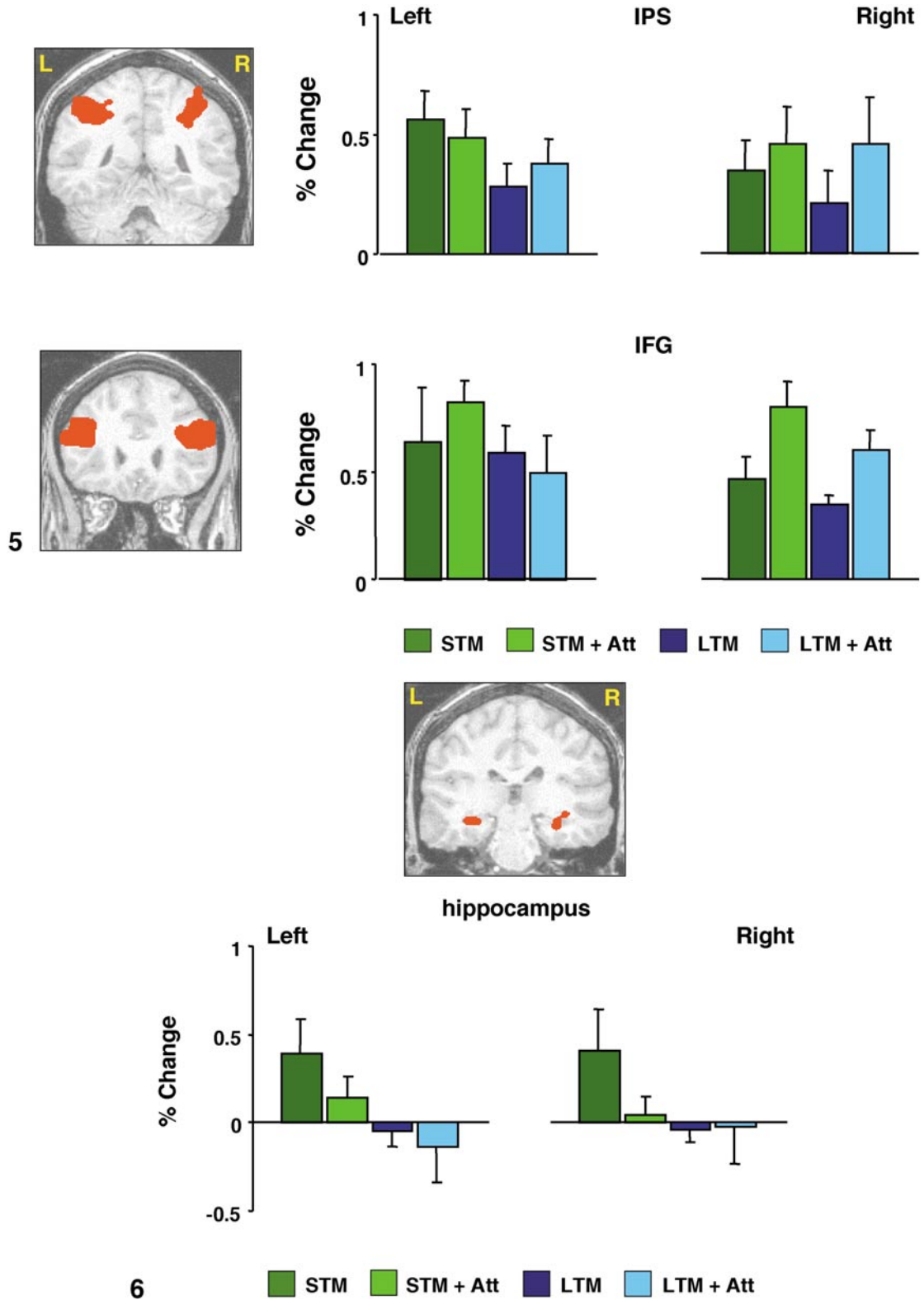
**FIG. 6.** Imagery responses in the hippocampus. (Top) Location of activation, illustrated in a coronal section from a single subject. Voxels shown in color demonstrated a significant imagery effect ($P < 0.001$). (Bottom) Mean amplitudes of the fMRI signal are averaged across all subjects and all repetitions of task block in each subject. Bars, SEM.

**TABLE 3**

Regions Activated during Visual Imagery of Famous Faces

| Region | N | Numbers of voxels | X | Y | Z |
|---|---|---|---|---|---|
| L calcarine | 4 | 37 (12) | −8 (1) | 54 (4) | 8 (2) |
| R calcarine | 5 | 36 (8) | 12 (2) | 61 (3) | 5 (1) |
| L hippocampus | 6 | 17 (8) | −21 (2) | 28 (2) | −3 (2) |
| R hippocampus | 5 | 10 (3) | 25 (2) | 22 (2) | −10 (2) |
| L precuneus | 4 | 12 (5) | −10 (2) | 60 (4) | 39 (3) |
| R precuneus | 4 | 15 (5) | 10 (2) | 59 (3) | 44 (3) |
| L IPS | 6 | 32 (7) | −38 (2) | 37 (3) | 40 (2) |
| R IPS | 6 | 41 (14) | 45 (3) | 34 (3) | 39 (1) |
| L IFG | 8 | 63 (14) | −37 (1) | −30 (2) | 27 (2) |
| R IFG | 7 | 56 (10) | 40 (1) | −26 (3) | 27 (2) |

*Note.* Volumes were calculated before spatial normalization. Coordinates are in the normalized space of the brain atlas of Talairach and Tournoux (1988). *N,* number of subjects in whom each region was identified. The mean for each region volume is calculated only for these subjects. Standard errors of the mean are indicated in parentheses.

compared with the imagery control condition, we identified several regions of interest, including the calcarine, hippocampus, precuneus, IPS, and IFG (see Table 3). We present the data according to the differential effects of memory and attention during imagery, respectively.

*Imagery from STM evoked stronger activation.* Figures 4 and 5 show the imagery activation in the calcarine, precuneus, IPS, and IFG. Visual imagery of famous faces generated from both STM and LTM evoked activation in these regions. Interestingly, in all these regions, as in face-selective regions described above, the activation during imagery generated from STM was stronger than the activation during imagery from LTM ($P < 0.01$; in each region data were pooled from both hemispheres). Contrary to our prediction, when subjects were attending to specific facial features of the imagined faces, this additional attention requirement did not result in increased activation in these ROIs.

We also found activation during imagery in the hippocampus (Fig. 6). In both hemispheres, imagery generated from STM evoked stronger activation than imagery from LTM ($P < 0.001$). Although the imagery from STM condition was preceded by visual presentation of the faces to be imagined, the activation was observed during the imagery epochs (i.e., retrieval) and not during encoding of those faces.

*Differential effects of focal attention during imagery.* Differential effects of focal attention during visual imagery of famous faces, as manifested by increased activation, were found in the right IPS and right IFG, regions previously implicated in many attention, memory, and imagery tasks (Fig. 5). In the right IPS and right IFG, the activation evoked during the imagery conditions that required focal attention to features was significantly higher than the activation during the imagery conditions that did not require focal attention ($P < 0.0001$). This increased activation owing to focal attention was observed during imagery generated from both STM and LTM and was thus independent of memory type.

*Visual response within the imagery network.* The visual response to famous faces was defined by the contrast of perception versus perception control. This contrast was set at a significance level of $P < 0.0001$ (see above). When we looked at the visual response in the calcarine, hippocampus, precuneus, IPS, and IFG, we did not find significant visual activa-

tion in these regions. The imagery response, however, was defined based on the contrast of visual imagery versus the imagery control condition, with a lower threshold ($P < 0.001$). When extracting the amplitude of the fMRI signal within these imagery-responsive regions, we also observed some responses during the visual *perception* condition.

## DISCUSSION

In the present study we investigated the neural systems that mediate the generation of visual images from STM and LTM and the effects of focal attention to features of visual mental images. Using passive viewing of famous faces in the perception condition, we found activation in the inferior occipital gyri, the lateral fusiform gyri, the STS, and the amygdala. Visual imagery of famous faces activated small subsets of these visually responsive regions. Moreover, visual imagery of famous faces activated a network of regions composed of bilateral calcarine, hippocampus, precuneus, IPS, and IFG. In all these regions, imagery generated from STM evoked more activation than imagery from LTM. During imagery from both STM and LTM, focusing attention on features of the imagined faces resulted in increased activation in the right IPS and right IFG.

The visual response evoked by famous faces revealed, as predicted, activation in multiple regions of the distributed neural system for face perception (Haxby *et al.,* 2000). Consistent with numerous neuroimaging studies of unfamiliar faces, we found activation in the inferior occipital gyri and the fusiform gyri, the extrastriate regions that mediate face recognition (Kanwisher *et al.,* 1997; McCarthy *et al.,* 1997; Gauthier *et al.,* 1999; Haxby *et al.,* 1999; Ishai *et al.,* 1999, 2000b). We also found activation in the STS and the amygdala, regions that mediate the processing of information relevant to social communication, for example, eye gaze direction (Puce *et al.,* 1999; Hoffman and Haxby, 2000) and facial expression (Breiter *et al.,* 1996; Morris *et al.,* 1996; Phillips *et al.,* 1997). Although our stimuli were gray-scale photographs of celebrities with neutral expressions, and the task was passive viewing, we observed amygdalar activation in all subjects. Our finding might be related to the affective component of viewing good-looking faces (see Appendix), as sug-

gested by a recent fMRI study in which "beautiful" faces evoked activation in the amygdala (Aharon *et al.,* 2001).

Previous functional brain imaging studies of familiar faces have used a variety of stimuli (e.g., celebrities, personally familiar faces, newly learned faces) and tasks, yet have found activation in similar visual areas that were activated by unfamiliar faces, most consistently in the fusiform gyrus (Sergent *et al.,* 1992; Gorno-Tempini *et al.,* 1998; Dubois *et al.,* 1999; Leveroni *et al.,* 2000; Nakamura *et al.,* 2000; Campanella *et al.,* 2001; Gorno-Tempini and Price, 2001; Rossion *et al.,* 2001; Shah *et al.,* 2001). In some studies, activation was found in an anterior middle temporal region, the locus proposed for the analysis of unique semantic attributes (Sergent *et al.,* 1992; Gorno-Tempini *et al.,* 1998; Leveroni *et al.,* 2000; Nakamura *et al.,* 2000; Gorno-Tempini and Price, 2001). It is of interest that activation in this anterior middle temporal region was found only when familiar and unfamiliar faces were directly compared. Since our experimental design did not include unfamiliar faces, and the visual response was defined by the contrast of famous faces versus scrambled faces, the lack of activation in the anterior middle temporal area in our study is not necessarily inconsistent with the above-mentioned reports.

Visual imagery of famous faces evoked activation in small subsets of the regions activated during perception, namely in the fusiform gyri, the STS, and the amygdala. Previously, we found that visual imagery of faces and other objects activated small clusters in the ventral temporal regions that showed category-related activation during perception (Ishai *et al.,* 2000a). Because imagery evoked activity in small portions of the regions that participate in perception, it is possible that stored information evoked by imagery is simply weaker than equivalent representations evoked by actual visual input. Alternatively, only a specific subset of cortical regions may be dedicated to mental imagery, allowing perception and imagery to operate simultaneously. Consistent with our previous report (Ishai *et al.,* 2000a), we did not find activation during imagery of famous faces in the ventral occipital cortex, suggesting that this cortex is less involved than ventral temporal cortex in the generation of complex visual images.

Our results suggest that sensory representations of faces stored in the lateral fusiform, the STS, and the amygdala are reactivated during the generation of visual images. The view that the neurons that "see" are also the neurons that "remember" is supported by early evidence that sensory regions in the temporal lobe are associated with memory retrieval (Penfield and Perot, 1963). Moreover, studies in nonhuman primates have implicated the temporal lobe as the memory storehouse for visual representations of complex stimuli (e.g., Mishkin, 1982; Miyashita and Chang, 1988; Miyashita, 1988). Finally, recent electrophysiologic and functional brain imaging studies have reported content-specific activation in sensory areas during imagery and memory retrieval (Ishai *et al.,* 2000a; Kreiman *et al.,* 2000; O'Craven and Kanwisher, 2000; Wheeler *et al.,* 2000).

Visual imagery of famous faces, compared with the imagery control condition, activated a network of regions, including the calcarine, hippocampus, precuneus, IPS, and IFG. We previously reported a similar network of regions implicated in the "top-down" control of generating and maintaining visual images of faces and other objects (Ishai *et al.,* 2000a). In the parietal lobe, visual imagery evoked activation in the IPS and the superior parietal lobule, regions involved in a variety of attention tasks (Nobre *et al.,* 1997; Corbetta *et al.,* 1998; Kastner *et al.,* 1999; Wojciulik and Kanwisher, 1999). Moreover, imagery activated the precuneus, a region involved in retrieval from episodic memory during memory-related imagery (Fletcher *et al.,* 1995; Ishai *et al.,* 2000a). In the frontal lobe, visual imagery of famous faces activated the inferior frontal gyri, regions involved in visual working memory (Courtney *et al.,* 1997, 1998; Petit *et al.,* 1998) and visual imagery (Ishai *et al.,* 2000a). It thus appears that visual imagery of faces (and objects) may be implemented by content-related responses in small sectors of visual cortex, controlled by frontal and parietal cortical networks shared with other cognitive operations, such as memory and attention. Similar conclusions were reached in a study of motion imagery (Goebel *et al.,* 1998) that found activation in a network composed of motion-sensitive regions MT/MST and prefrontal areas (FEF and BA 9/46).

Interestingly, we found that in all the cortical regions that responded during visual imagery (the fusiform, STS, amygdala, hippocampus, calcarine, precuneus, IPS, and IFG), the activation evoked during generation of mental images from STM was stronger than the activation evoked during imagery from LTM. When subjects were presented with specific pictures of celebrities and memorized them prior to the imagery task, the brain activity during imagery was stronger, suggesting that maintaining a trace in a "working memory buffer" for several seconds likely mediates the generation of visual images. This finding is reminiscent of previous psychophysical studies, which found that memorizing (or encoding) pictorial information presented shortly before the imagery task enhanced performance. Furthermore, this imagery-induced facilitation was mediated by a stimulus-specific short-term memory trace (Ishai and Sagi, 1995, 1997a,b). An alternative explanation is that subjects generated more vivid images in the STM conditions and vaguer images in the LTM conditions. This explanation, however, is not supported by the behavioral data. Our subjects reported generating "clear and reasonably vivid" images of faces during both the STM and the LTM imagery conditions. Moreover, seeing faces before imagining them did not result in faster reaction times in the STM imagery conditions, consistent with a previous behavioral study, in which prior perception of faces failed to prime imagery of faces (Cabeza *et al.,* 1997). Thus, we think that the greater activation during STM imagery compared to LTM imagery is due to memory processes per se rather than the vividness of the images.

Visual imagery of famous faces generated from STM evoked bilateral activation in the hippocampus. Previous studies indicated the involvement of the hippocampus during encoding of novel faces (Haxby *et al.,* 1996) and during the encoding of novel face–name associations (Sperling *et al.,* 2001), concurrent with its role in associative memory processing (e.g., Dolan and Fletcher, 1997). Moreover, a recent fMRI study reported activation in the hippocampus during active maintenance (or rehearsal) of novel faces in working memory (Ranganath and D'Espositio, 2001). Finally, our results suggest that the hippocampus is also activated during the retrieval of mental images. In essence, each retrieval

experience is also a reencoding experience. Thus, it is likely that during the STM imagery conditions subjects reencoded the faces they were presented with shortly before.

Contrary to our expectation, we did not observe significant effects of focal attention during imagery in the extrastriate cortex. When subjects scrutinized their mental images and attended to specific features (eyes, lips, nose) of the imagined faces, we found increased activation only in the IPS and the IFG, regions previously implicated in the control of attention and retrieval from memory. Interestingly, the differential effect of attention was stronger in the right hemisphere. This hemispheric asymmetry is inconsistent with studies of focal versus global processing, in which the left hemisphere seems to play a dominant role (e.g., Delis *et al.,* 1983). However, it is consistent with reports on the localization of activation during sustained attention (e.g., Pardo *et al.,* 1990) and neuropsychological evidence that right-sided damage of parietal and frontal regions can produce neglect, a deficit in orienting attention to objects in the left visual hemifield (Mesulam, 1981).

We found evidence for calcarine activation during visual imagery of famous faces, which is in agreement with some previous reports of activation in early visual areas (Le Bihan *et al.,* 1993; Kosslyn *et al.,* 1993, 1995, 1996, 1999; Chen *et al.,* 1998; Klein *et al.,* 2000; Thompson *et al.,* 2001; Lambert *et al.,* 2002). Other studies, however, have not found activation in early visual areas during imagery (Roland *et al.,* 1987; Roland and Gulyas, 1995; Mellet *et al.,* 1995, 1996, 1998, 2000a,b; D'Esposito *et al.,* 1997; Ishai *et al.,* 2000a; Knauff *et al.,* 2000; Gulyas, 2001). As different researchers have used different tasks and/or had different baseline conditions, it is difficult to account for the conflicting findings. We suggest that the type of memory (short- or long-term) required for the generation of mental images is a crucial factor in the V1 debate. Our results indicated that imagery generated from STM evoked stronger activation than imagery from LTM in the calcarine. Indeed, a review of the studies reporting activation in V1 revealed that the great majority of the imagery tasks were based on recall from STM (e.g., Le Bihan *et al.,* 1993; Kosslyn *et al.,* 1995, 1996, 1999; Chen *et al.,* 1998; Goebel *et al.,* 1998; O'Craven and Kanwisher, 2000; Thompson *et al.,* 2001), whereas imagery tasks based on recall from LTM have not found activation in V1 (e.g., Roland *et al.,* 1987; Roland and Gulyas, 1995; Mellet *et al.,* 1995, 1996, 1998, 2000a,b; D'Esposito *et al.,* 1997; Ishai *et al.,* 2000a; Knauff *et al.,* 2000; Gulyas, 2001). It thus seems that maintaining a trace in a short-term buffer may be required for activation in the calcarine. A recent event-related fMRI study of animal imagery challenges our STM/LTM classification of activation in V1 (Klein *et al.,* 2000). In that study, subjects generated an image of an animal ("cat") and then evaluated the image by answering either a concrete question ("has pointy ears") or an abstract question ("is affectionate"). Although the imagery task was based on LTM, both concrete and abstract trials revealed transient activation in V1. Interestingly, this finding is consistent with a model suggested by Sakai and Miyashita (1994), according to which focal attention to mental images would recruit V1. We did not, however, observe any differential patterns of activation owing to focusing attention on features of the imagined faces. It is unclear whether the lack of attentional effects during imagery in the calcarine was due to the content of the images (i.e., famous faces). Similarly, it is unclear whether imagery effects observed in the

calcarine are attributable to the content of the images (simple geometric forms) or the effects of attention (e.g., Kosslyn *et al.,* 1993). Future studies are needed to investigate the interaction of memory type with attention.

## APPENDIX

### List of Famous Faces

| | | |
|---|---|---|
| Al Pacino | Geena Davis | Mia Farrow |
| Alec Baldwin | George Clooney | Michael Douglas |
| Alicia Silverstone | Gillian Anderson | Michael J. Fox |
| Andy Garcia | Glenn Close | Michael Jackson |
| Angelina Jolie | Goldie Hawn | Michael Keaton |
| Annete Bening | Gwyneth Paltrow | Michelle Pfeifer |
| Anthony Hopkins | Halle Berry | Mike Myers |
| Antonio Banderas | Harrison Ford | Minnie Driver |
| Ashley Judd | Heather Locklear | Morgan Freeman |
| Barbara Striesand | Helen Hunt | Naomi Campbell |
| Ben Affleck | Hugh Grant | Natalie Portman |
| Ben Kingsley | Jack Nicholson | Nicholas Cage |
| Bette Midler | Jacqueline Bisette | Nicole Kidman |
| Bill Clinton | Jane Fonda | Noah Wyle |
| Bill Cosby | Jane Seymour | Patrick Swayze |
| Bill Paxton | Jay Leno | Paul Newman |
| Billy Zane | Jeff Bridges | Penelope Cruz |
| Brad Pitt | Jennifer Aniston | Pierce Brosnan |
| Brendan Fraser | Jennifer Lopez | Ralph Fiennes |
| Brooke Shields | Jennifer Love Hewitt | Rebecca Demornay |
| Bruce Willis | Jim Carey | Rene Russo |
| Calista Flockhart | Jodie Foster | Renee Zellweger |
| Cameron Diaz | John Cusack | Richard Gere |
| Carmen Electra | John Malkovich | Ricky Martin |
| Celine Dion | John Travolta | Robert DeNiro |
| Charlize Theron | Johny Depp | Robert Downey Jr. |
| Chaterine Zeta Jones | Jude Law | Robert Duvall |
| Cher | Julia Ormond | Robert Redford |
| Chris O'Donnell | Julia Roberts | Robin Williams |
| Chrisitina Ricci | Julianne Moore | Rosanna Arquette |
| Christian Bale | Kate Moss | Rupert Everett |
| Christian Slater | Kate Winslet | Russell Crowe |
| Christina Aguilera | Kevin Bacon | Salma Hayek |
| Christy Turlington | Kevin Kostner | Samuel L. Jackson |
| Cindy Crawford | Kevin Spacey | Sandra Bullock |
| Claire Danes | Kiano Reeves | Sarah Jessica Parker |
| Claudia Schiffer | Kim Basinger | Sarah Michelle Gellar |
| Clint Eastwood | Kim Cattrall | Sean Connery |
| Courtney Cox | Kristin Scott Thomas | Sean Penn |
| Cuba Gooding Jr. | Laetitia Casta | Sela Ward |
| Danny De Vito | Leonardo DiCaprio | Sharon Stone |
| David Duchovney | Liam Neeson | Sigourney Weaver |
| David Hasselhoff | Lisa Kudrow | Sophie Marceau |
| David James Elliott | Liv Tyler | Susanne Sarandon |
| Denise Richards | Madeleine Stowe | Sylvester Stallone |
| Demi Moore | Madonna | Timothy Hutton |
| Denzel Washington | Mariah Carey | Tom Cruise |
| Diane Keaton | Marilyn Monroe | Tom Hanks |
| Diane Lane | Marisa Tomei | Tommy Lee Jones |
| Don Johnson | Marlon Brando | Tyra Banks |
| Drew Barrymore | Martin Sheen | Uma Thurman |
| Dustin Hoffman | Matt Damon | Val Kilmer |
| Dylan McDermott | Matt Dillon | Vanessa L. Williams |
| Ed Harris | Matthew McConaghey | Warren Beatty |
| Eddie Murphy | Meg Ryan | Whoopi Goldberg |
| Elizabeth Hurley | Mel Gibson | Will Smith |
| Emma Thompson | Melanie Griffith | Winona Rider |
| Ewan McGregor | Meryl Streep | Woody Allen |
| Freddie Prinze Jr. | | |

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