

Face-Specific Processing in the Human Fusiform Gyrus

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Abstract

■ The perception of faces is sometimes regarded as a specialized task involving discrete brain regions. In an attempt to identify face-specific cortex, we used functional magnetic resonance imaging (fMRI) to measure activation evoked by faces presented in a continuously changing montage of common objects or in a similar montage of nonobjects. Bilateral regions of the posterior fusiform gyrus were activated by faces viewed among nonobjects, but when viewed among objects, faces activated only a focal right fusiform region. To determine

whether this focal activation would occur for another category of familiar stimuli, subjects viewed flowers presented among nonobjects and objects. While flowers among nonobjects evoked bilateral fusiform activation, flowers among objects evoked no activation. These results demonstrate that both faces and flowers activate large and partially overlapping regions of inferior extrastriate cortex. A smaller region, located primarily in the right lateral fusiform gyrus, is activated specifically by faces. ■

INTRODUCTION

There are several reasons for believing that human faces are a biologically important class of visual objects that may be processed by specialized brain mechanisms (reviewed by Bruce & Humphreys, 1994). Damage to occipitotemporal cortex may produce an inability to recognize familiar faces (Meadows, 1974; Whiteley & Warrington, 1977; Damasio, Damasio, & Van Hoesen, 1982; Damasio, Tranel, & Damasio, 1990) with little or no deficit in recognizing other categories of objects (Farah, 1994; Newcombe, Mehta, & de Haan, 1994). Single-unit recordings from the temporal lobe of monkeys reveal cells that respond selectively to faces or face components (Perrett, Hietanen, Oram, & Benson, 1992; Gross, 1992; Wang, Tanaka, & Tanifuji, 1996). Recordings in patients with chronically implanted electrodes demonstrate that discrete regions of inferior occipito-temporal cortex generate short-latency field potentials to faces but not to scrambled faces, letter strings, animals, or cars (Allison, Ginter, et al., 1994; Allison, McCarthy, Nobre, Puce, & Belger, 1994; Nobre, Allison, & McCarthy, 1994).

Positron emission tomography (PET) and fMRI demonstrate that regions of occipito-temporal cortex are activated by a variety of face-processing tasks (Sergent, Ohta, & MacDonald, 1992; Haxby et al., 1994; Clark et al., 1995; Puce, Allison, Gore, & McCarthy, 1995). However, these regions are also activated by objects (Malach et al., 1995; Schacter et al., 1995; Köhler, Kapur, Moscovitch, Winocur, & Houle, 1995; Kanwisher, Woods, Iacoboni, & Mazziotta, 1997); hence activation by faces may simply reflect gen-

eral object processing. Presented in isolation, faces may engender both specific and general object processing. We reasoned that a face-specific processing region might be revealed only if the general object recognition system was occupied by concurrent object processing. To evaluate this possibility, faces were periodically presented within a continuously changing montage of common objects and nonobjects on the assumption that nonobjects would not engage object recognition processes but would control for physical stimulus characteristics such as luminance and spatial frequency. Face-specific processing regions would appear as a subset of a more extensive activation evoked in the general object recognition system. To determine whether within-category processing of *any* well-known object category produces similar results as faces, the experiment was repeated substituting flowers for faces. Flowers were predicted to activate the general object recognition system when presented among nonobjects but not when presented among objects. A preliminary report of these results has been presented (McCarthy, Puce, Gore, & Allison, 1996).

RESULTS

Figure 1a demonstrates that faces among nonobjects evoked extensive inferior brain activation with the largest number of activated voxels occurring in slices 4 and 5. Figure 1b demonstrates that flowers among nonobjects also produced extensive inferior brain activation. Figure 1c shows that faces among nonobjects evoked more activation in the right hemisphere, particularly in

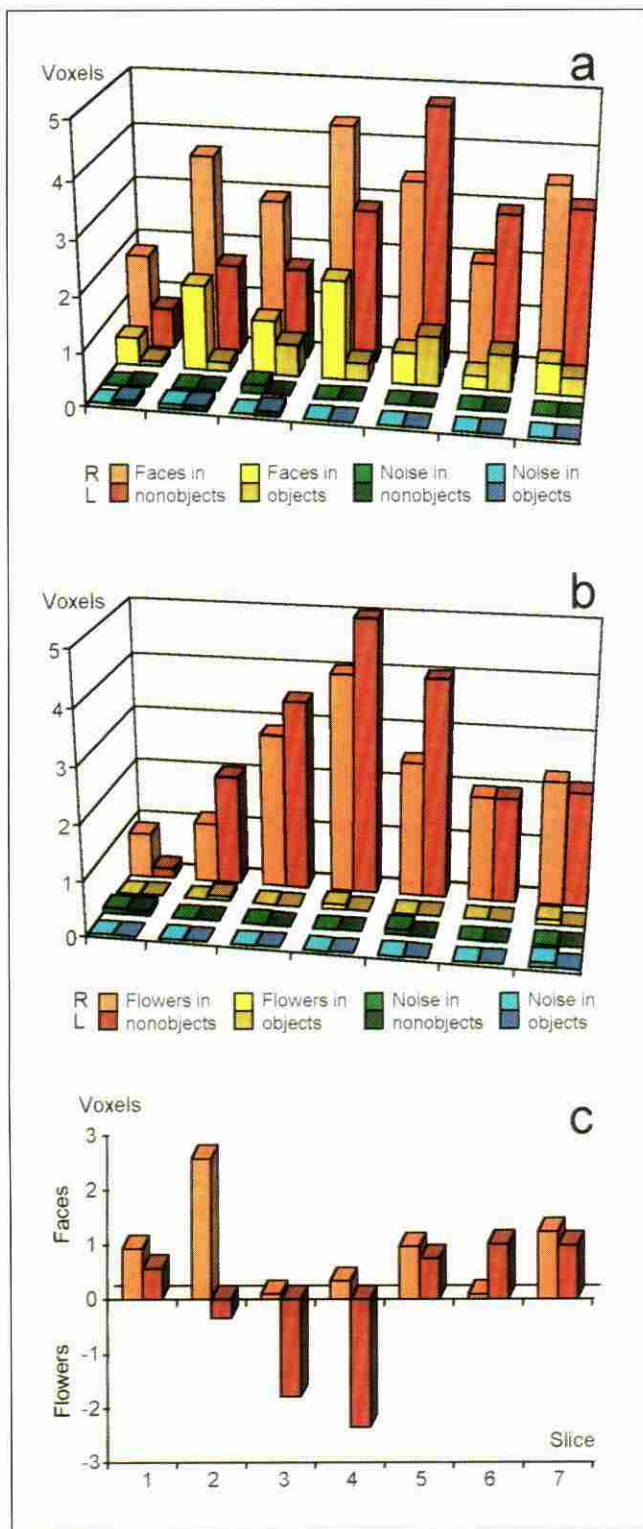


Figure 1. Mean number of voxels (averaged across all subjects) activated by faces (a) and by flowers (b) in right and left inferior occipito-temporal cortex. This measure includes all voxels within and inferior to the inferior temporal gyrus and represents 86% of all activated voxels. Slice 1 was the most anterior, and slice 7 was the most posterior. Average anterior-posterior locations in the atlas of Talairach & Tournoux (1988) were, for slices 1 through 7 respectively, $y = -40, -47, -54, -61, -68, -75, -82$. (c) Differences in activation (mean voxel count) by faces and flowers among nonobjects. A positive difference denotes greater activation by faces than flowers, whereas a negative difference denotes greater activation by flowers. The largest effects were in slice 2, where activation by faces was greater than for flowers in the right hemisphere, and in slice 4, where activation by flowers was greater than for faces in the left hemisphere.

slice 2. Flowers among nonobjects evoked more activation in the left hemisphere in slices 3 and 4. While faces and flowers both activated slices 5 through 7, the difference in their patterns of activation was small.

These results confirm our expectation that both object categories produce strong inferior occipito-temporal activation during concurrent nonobject processing. Of critical importance is whether periodic activation can be measured during concurrent object processing. Figure 1a shows activation by faces among objects, with the greatest activation occurring in the right hemisphere in slices 2 and 4. These voxels were a subset of those activated by faces among nonobjects.¹ An estimate of noise was calculated for the nonobject and object conditions; voxels activated by faces among objects were well above this noise level (Figure 1a). In marked contrast, flowers among objects produced no activation that exceeded the noise level (Figure 1b).

Figure 2 illustrates activation by faces for four individual subjects and the across-subjects average for slice 2, which produced the largest relative face activation (Figure 1c). Faces among nonobjects produced activation of the right fusiform gyrus and produced lesser activation of the left fusiform gyrus (Figure 2b and c). Faces among objects activated a smaller region of the right fusiform gyrus but did not activate the left fusiform gyrus (Figure 2e and f).

Figure 3 presents a similar comparison for activation by flowers for slice 4, which produced the largest relative flower activation (Figure 1c). Activation of the fusiform gyri and, in one subject, activation of the intraparietal sulci was evoked by flowers among nonobjects (Figure 3b and c). However, flowers among objects evoked no fusiform activation in this or any other slice (Figure 3e and f).

This pattern of activation is summarized in Table 1: (1) When viewed among nonobjects, faces activated the right hemisphere more than the left, and flowers activated the left hemisphere more than the right, (2) when viewed among objects, faces activated a focal right fusiform region while flowers evoked no activation in either hemisphere, and (3) the greatest activation by faces occurred in the lateral fusiform gyrus, while the greatest activation by flowers occurred in the midfusiform sulcus. The medial fusiform gyrus was only slightly activated by

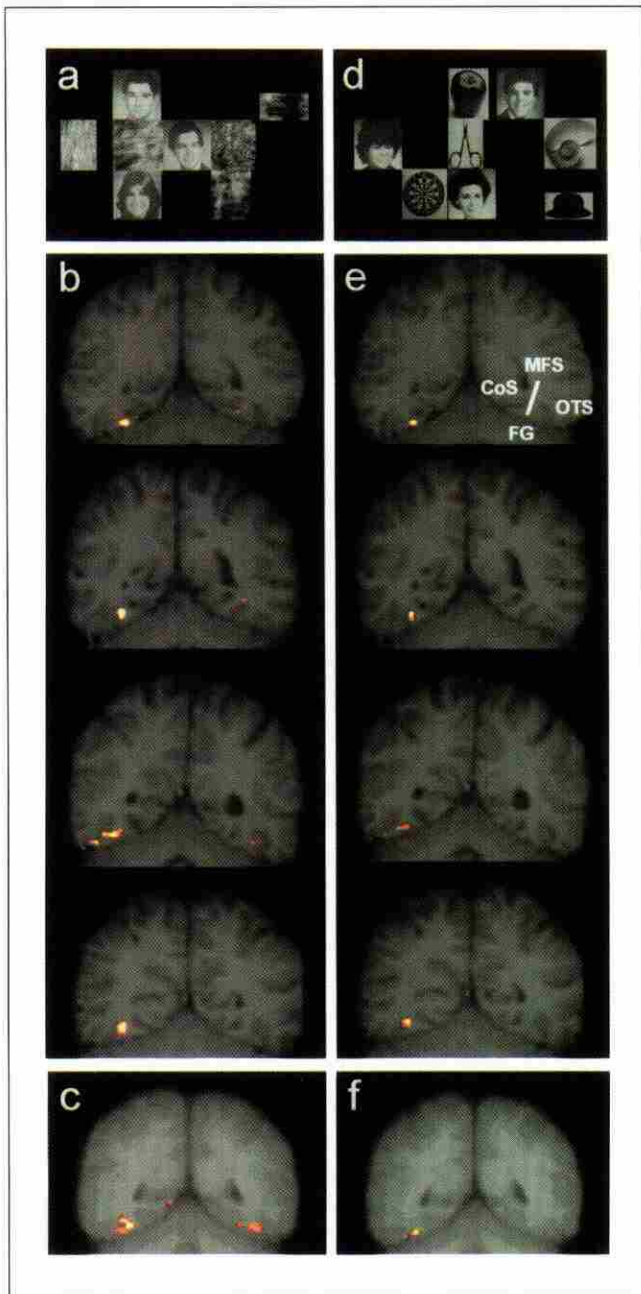


Figure 2. (a) Faces among nonobjects. At any instant a random subset of 15 possible locations was occupied by faces and nonobjects or by nonobjects alone. Nonobjects were presented continuously while faces appeared periodically. (b) Activation by faces among nonobjects for four subjects (coronal section, slice 2, T -values > 1.96). The right side of the brain appears on the left side of the image. (c) Across-subjects average activation by faces among nonobjects for slice 2. (d) Faces among objects. (e) Activation by faces among objects; subjects and slice are the same as in (b). The fusiform gyrus (FG) is bounded medially by the collateral sulcus (CoS) and laterally by the occipito-temporal sulcus (OTS); it is divided into medial and lateral portions by the midfusiform sulcus (MFS). (f) Across-subjects average activation by faces among objects for slice 2.

faces among nonobjects and not at all by faces or flowers among objects.

DISCUSSION

These results demonstrate that faces viewed within a complex scene of continuously changing objects activate a small region of extrastriate visual cortex, limited primarily to the right fusiform gyrus (Table 1). This conclusion supports the argument that faces are treated differently from nonface objects by the visual system and are processed in a specialized region evident when the general object recognition system is occupied.

It has long been thought that the right hemisphere is more engaged in face processing than is the left hemisphere. Behavioral studies demonstrate a right-hemisphere advantage for face recognition (reviewed by Rhodes, 1993). While lesions that produce prosopagnosia are often bilateral, lesions limited to the right occipito-temporal region can also produce prosopagnosia (Whiteley & Warrington, 1977; Damasio et al., 1990; De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994). PET (Horwitz et al., 1992; Haxby, Ungerleider, Horwitz, Rapoport, & Grady, 1995), fMRI (Puce et al., 1995; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Kanwisher, McDermott, & Chun, 1996; Kanwisher, Chun, McDermott, & Hamilton, 1996), and scalp-recorded evoked potential (Bentin, Allison, Puce, Perez, & McCarthy, 1996) studies reveal greater activation by faces in the right than the left occipito-temporal region. In this study, the volume of cortex activated by faces among nonobjects was approximately twice as large in the right than in the left hemisphere. The smaller left-hemisphere activation was further diminished for faces among objects (Table 1), suggesting that the right-hemisphere advantage for face processing is especially strong in complex visual environments.

It has been suggested that face recognition is a special case of object processing requiring within-category (subordinate) discrimination of visually similar objects (e.g., Damasio et al., 1982; Gauthier et al., 1996; reviewed by Logothetis & Sheinberg, 1996). In this study we used unfamiliar faces and flowers in a passive viewing task that did not require subordinate-level processing of either category. Kanwisher et al. (1996) examined this issue explicitly in an fMRI study and found that a region of the right fusiform gyrus, similar in location to the region described here, was more activated by faces than by hands even when subordinate-level identification of hands was more difficult than identification of faces. While we cannot rule out the possibility that some of the activation to faces seen in this study was due to differences in depth of processing rather than to face-specific processing, we regard this explanation as unlikely.

The anatomical configuration of face-specific cortex is unclear. Each region could be composed of face-specific

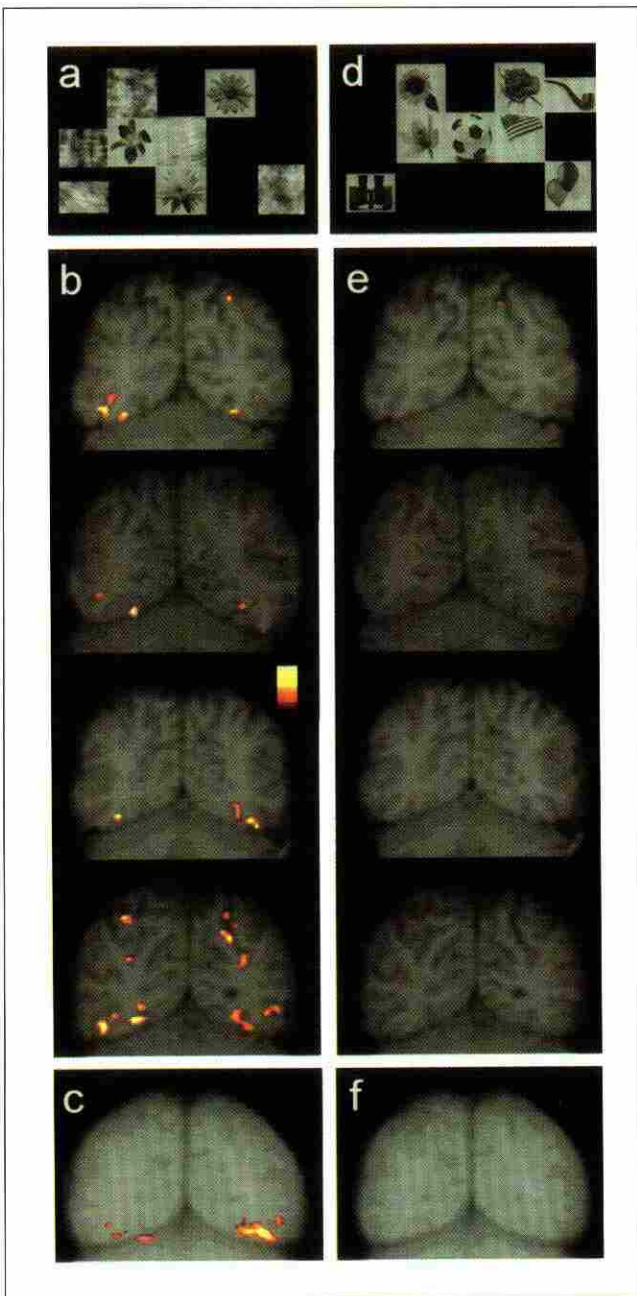


Figure 3. (a) Flowers among nonobjects. (b) Activation by flowers among nonobjects for four subjects (slice 4). (c) Across-subjects average activation by flowers among nonobjects for slice 4. (d) Flowers among objects. (e) Activation by flowers among objects; subjects and slice the same as in (b). (f) Across-subjects average activation by flowers among objects for slice 4.

columns of cells 0.4 to 1.0 mm in diameter like those in monkeys (Fujita, Tanaka, Ito, & Cheng, 1992; Wang et al., 1996), interspersed among columns of different selectivity. Such a dispersed pattern of activation might be expected to produce a random stippling of activation throughout the fusiform gyrus rather than the focal activation that we found. Alternatively, face-specific regions could occur in patches of cortex (perhaps composed of clusters of face-specific columns), an arrangement sug-

gested by face-sensitive patches of cortex in monkey temporal lobe (Harries & Perrett, 1991). The right hemisphere activations in Figure 2e suggest elongated patches of face-specific cortex located in the midfusiform sulcus and lateral fusiform gyrus.

We conclude that faces are perceived at least in part by a separate processing stream within the ventral object recognition system (Ungerleider & Mishkin, 1982; Livingstone & Hubel, 1988; Merigan & Maunsell, 1993). In humans a major component of this stream occupies lateral portions of the right fusiform gyrus.

METHODS

Twelve volunteer subjects (six males), ranging in age from 22 to 43 years, participated in this study. Eleven subjects were right handed and one was ambidextrous. The protocol was approved by the Human Investigation Committee of Yale University School of Medicine, and informed consent was obtained. A 1.5T General Electric Signa scanner with a standard quadrature head coil and ANMR echoplanar subsystem was used. The subject's head was positioned along the canthomeatal line and immobilized using a vacuum cushion and a forehead strap. T_1 -weighted sagittal scans were used to select seven contiguous 7-mm coronal slices beginning at the posterior edge of the splenium. Functional images were acquired using a gradient-echo echoplanar sequence ($T_R = 1500$, $T_E = 45$, $\alpha = 60^\circ$, NEX = 1, voxel size = $3.2 \times 3.2 \times 7$ mm). Each imaging run consisted of 128 images per slice (196-sec scan time).

Four categories of gray-scale stimuli were back-projected onto a translucent screen that subjects viewed through a mirror mounted on the head coil: (1) Male and female faces scanned from college yearbooks (Figure 2a), (2) stock images of individual common objects, fruits, and vegetables (Figure 2d), (3) nonobjects generated by computing a Fourier transform of each object image, randomly scrambling its phase spectrum while preserving its frequency spectrum and then performing an inverse transform (Figure 2a), and (4) stock images of individual flowers (Figure 3a). The average intensity and contrast of stimuli were equalized across the four stimulus categories. Each run of an activation task lasted 196 sec and consisted of approximately 1100 stimuli, each presented for 500 to 1000 msec at 1 of 15 screen locations. The onsets and offsets of individual stimuli were asynchronous, resulting in a continuously changing montage in which an average of 5.4 stimuli were visible every second. Individual stimuli fit within a $1.85^\circ \times 1.85^\circ$ area, and the complete display subtended horizontal and vertical angles of $9.3^\circ \times 5.6^\circ$.

Eight runs of the face task were acquired in the first imaging session; there were four runs of objects and four runs of nonobjects. In all runs, faces appeared among the object or nonobject stimuli at predetermined periods. In half of the runs, faces appeared for a 6-sec period and

Table 1. Average volumes of activation (in mm³) in the right (R) and left (L) fusiform gyrus.^a

	Faces in nonobjects		Faces in objects		Flowers in nonobjects		Flowers in objects	
	R	L	R	L	R	L	R	L
Medial fusiform gyrus	60	0	0	0	13	156	0	0
Midfusiform sulcus	197	149	143	18	209	254	0	0
Lateral fusiform gyrus	299	113	137	12	91	59	0	0
Total	556	262	280	30	313	469	0	0

^a Volume calculations based on voxel counts from average *t*-maps ($t > 1.96$). The Talairach (x, y, z) coordinates for the centroids of activation in the fusiform gyrus were: Faces among nonobjects (R: 36, -52, -19, L: -35, -56, -17); Faces among objects (R: 40, -59, -22, L: -40, -55, -15); Flowers among nonobjects (R: 30, -54, -15, L: -30, -59, -20).

then disappeared for 6 sec, resulting in a 12-sec cycle time (15 to 16 cycles per run). In the remaining runs, faces appeared and disappeared every 8.73 sec, resulting in a 17.46-sec cycle time (10 to 11 cycles per run). The total number of visible stimuli did not change with the inclusion of the periodic face stimuli. In a second imaging session, flowers substituted for faces using the same object and nonobject backgrounds.

For the 12-sec cycle, the three images per slice acquired at the end of each face or flower 6-sec "on" period was compared to the three images acquired at the end of each 6-sec "off" period using an unpaired *t*-test on a voxel-by-voxel basis. Four images per period were compared for the 17.46-sec cycle. For each subject, average *t*-maps were computed for faces and flowers among objects and nonobjects. Voxels exceeding a *t*-value of 1.96 were counted for each task, slice, and hemisphere. To estimate the number of false positive or noise voxels, a second set of *t*-maps was computed in which the 17.46-sec cycle runs were analyzed using images selected according to the schedule of a 12-sec cycle run. Similarly, the 12-sec cycle runs were analyzed using images selected according to the schedule for a 17.46-sec cycle. Thus the grouping of images was not synchronized to stimulus on and off periods, but periodic noise could be measured. Across-subjects *t*-maps were also computed. Prior to averaging, *t*-maps for each subject were translated, stretched, and rotated to align gyri and sulci to a reference image set. Alignment factors were calculated using high-resolution anatomical images without regard to the functional activations. Alignments were performed separately for each hemisphere and for each slice.

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Notes

1. For those voxels activated by faces among objects, the corresponding voxel or its immediate neighbor was activated by faces among nonobjects 88% of the time for the right hemisphere and 65% of the time for the left hemisphere. Within the right hemisphere, the overlap was 100% for slice 2.

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