

The Representation of Objects in the Human Occipital and Temporal Cortex

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Abstract

■ Recently, we identified, using fMRI, three bilateral regions in the ventral temporal cortex that responded preferentially to faces, houses, and chairs [Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences, U.S.A.*, 96, 9379–9384]. Here, we report differential patterns of activation, similar to those seen in the ventral temporal cortex, in bilateral regions of the ventral occipital cortex. We also found category-related responses in the dorsal occipital cortex and in the superior temporal sulcus. Moreover, rather than activating discrete, segregated areas, each category was associated with

its own differential pattern of response across a broad expanse of cortex. The distributed patterns of response were similar across tasks (passive viewing, delayed matching) and presentation formats (photographs, line drawings). We propose that the representation of objects in the ventral visual pathway, including both occipital and temporal regions, is not restricted to small, highly selective patches of cortex but, instead, is a distributed representation of information about object form. Within this distributed system, the representation of faces appears to be less extensive as compared to the representations of nonface objects. ■

INTRODUCTION

Several brain imaging and electrophysiological recording studies in humans have reported discrete cortical regions in the posterior ventral temporal cortex that respond preferentially to faces (Haxby et al., 1999; Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997; Clark et al., 1996; Puce, Allison, Gore, & McCarthy, 1995; Puce, Allison, Asgari, Gore, & McCarthy, 1996; Allison, McCarthy, Nobre, Puce, & Begler, 1994), scenes/buildings (Haxby et al., 1999; Aguirre, Zarahn, & D'Esposito, 1998; Epstein & Kanwisher, 1998), letters (Polk & Farah, 1998; Puce et al., 1996), animals, tools (Chao, Haxby, & Martin, 1999; Martin, Wiggs, Ungerleider, & Haxby, 1996), and hands (Puce, Allison, & McCarthy, 1999). These findings have led to the interpretation that the ventral temporal cortex contains anatomically segregated modules that are category-specific (Puce et al., 1999; Aguirre et al., 1998; Kanwisher et al., 1997; Allison et al., 1994). Recently, we reported the existence of three regions in the ventral temporal cortex that responded preferentially to faces and to two categories of man-made objects, namely, houses and chairs (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999). The location of the face- and house-selective regions agreed with previous reports (e.g., Aguirre et al., 1998; Kanwisher et al., 1997). The arrangement of these regions had a topological organization that was highly consistent across subjects. Importantly, each category also evoked significant responses in the

regions that responded maximally to other stimuli and was associated with its own differential pattern of response in these other regions. Although the segregation of three regions with category-related responses could be interpreted as evidence for separate modules, the evidence for broad, overlapping, category-related patterns of response that extended across these regions led us to argue that the representation of an object is not restricted to the regions that respond maximally to that object but, rather, is distributed across a broader expanse of cortex. According to our model, the functional architecture of the ventral temporal cortex is based on a distributed representation of attributes of object form, in which attributes that are shared by members of a category tend to cluster together, thereby giving the appearance of category-specific modules.

Interestingly, regions that respond preferentially to faces, houses, animals, tools, and scenes have also been reported for the occipital cortex (Halgren et al. 1999; Haxby et al., 1999; Chao, Haxby, et al., 1999; Gauthier, Anderson, & Skudlarski, & Gore, 1999; Kanwisher et al., 1997; Perani et al., 1995; Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Martin et al., 1996), and may even be located within the earliest visual processing areas of medial occipital cortex (Chao, Haxby, et al., 1999; Martin et al., 1996). It is unclear, however, if the existence of category-related patterns of response in the occipital cortex indicates that the representations of categories or category-related features are segregated at this earlier

stage in visual processing or reflects a top-down influence of categorical segregation from later stages.

In this report, we examine the extent to which regions of occipital cortex demonstrate category-related patterns of response to faces, houses, and chairs and compare the category-related patterns of response in the occipital cortex to the patterns in the ventral temporal cortex that we reported earlier (Ishai et al., 1999). We chose chairs as a second category of man-made objects because they have no biological significance that might have led to the evolution of a specialized neural substrate for their perception. In particular, we asked: (1) Are there regions of the occipital lobe that respond preferentially to these categories of objects? (2) If so, are these regions less selective than those in the temporal lobe? (3) Is there any evidence that faces are represented differently from other objects?

RESULTS

In the following sections, data from two experiments will be discussed. In Experiment 1, subjects performed passive viewing and delayed match-to-sample tasks with gray-scale photographs of houses, faces, and chairs. In Experiment 2, subjects performed delayed matching tasks with gray-scale photographs and black and white line drawings of these object categories (see Experimental Procedure).

Behavioral Data

The behavioral data collected during scanning are shown in Table 1. As we reported earlier (Ishai et al., 1999), accuracy and reaction times on the delayed match-to-sample tasks did not differ for houses, faces, and chairs ($p > .2$ in all cases). For all categories, reaction times for line drawings were shorter than reaction times for photographs ($p < .001$), presumably because the sample and choice stimuli were presented at different viewing angles for photographs but not for line drawings.

We also recorded eye movements (see Ishai et al., 1999) while subjects performed the passive viewing and delayed match-to-sample tasks outside the MR scanner. During passive viewing, subjects made on average seven saccades during each 21-sec block (eight for houses, six for faces, five for chairs) with an average amplitude of 1.2° . During delayed matching, subjects made on average 31 saccades during each block (35 for houses, 29 for faces, 30 for chairs) with an average amplitude of 3.5° . These differences in number and amplitude of saccadic eye movements were not statistically significant ($p > .05$).

Imaging Data

Six bilateral regions in the ventral occipital and ventral temporal cortex were found that consistently showed

Table 1. Behavioral Data

	<i>Reaction time, msec</i>	<i>Accuracy, %</i>
<i>Experiment 1</i>		
Houses	1088 (46)	88 (2)
Faces	1125 (49)	90 (2)
Chairs	1119 (33)	86 (2)
<i>Experiment 2</i>		
Photographs		
Houses	1012 (33)	88 (2)
Faces	1061 (43)	93 (2)
Chairs	1052 (40)	92 (1)
Line drawings		
Houses	833 (36)	92 (3)
Faces	824 (56)	95 (1)
Chairs	786 (39)	96 (2)

Mean reaction times (msec) and accuracy (%). Standard errors of the mean (*SE*) are given in the parenthesis.

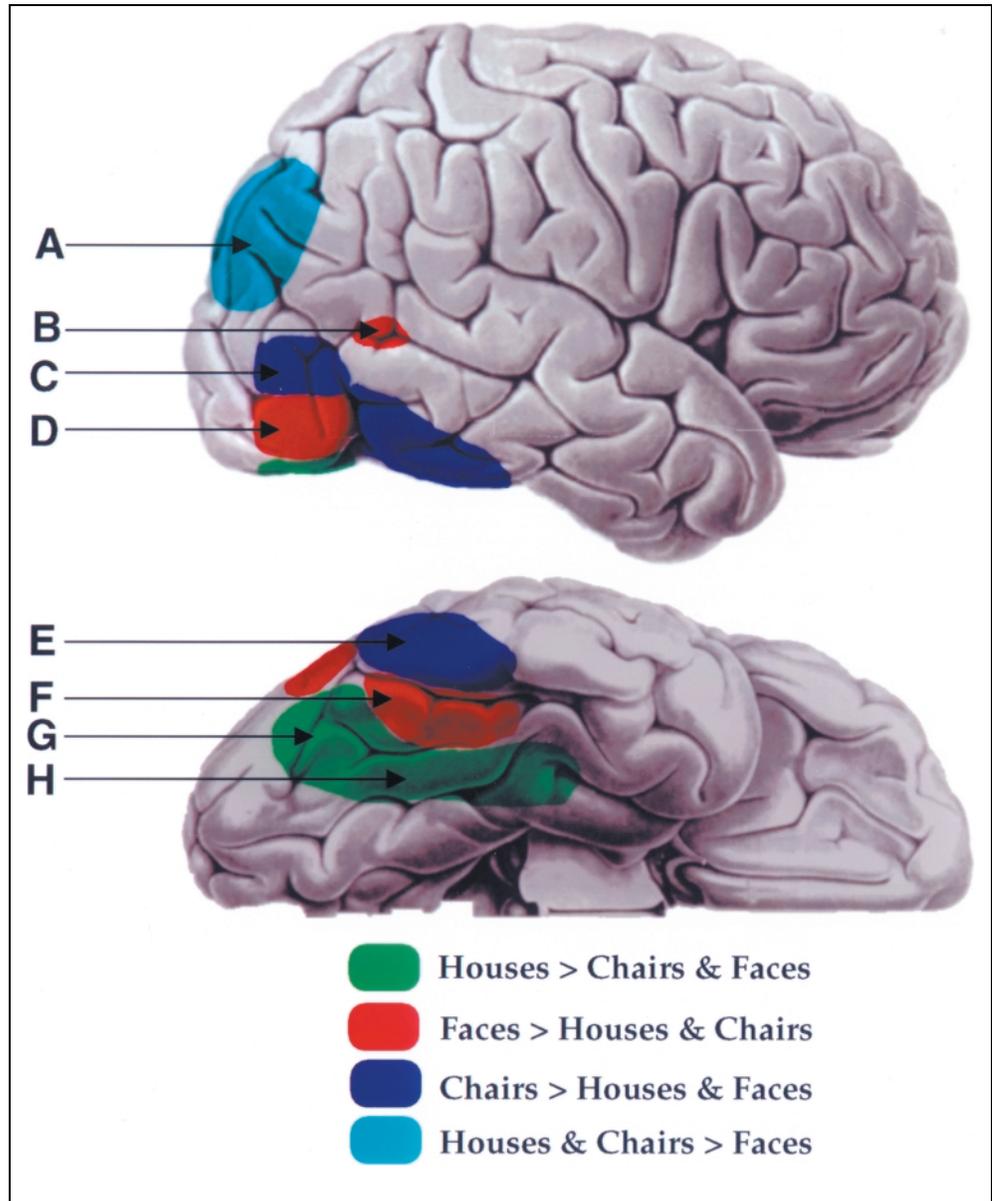
differential activations across subjects. Henceforth, these regions will be termed in the ventral temporal cortex: medial fusiform gyri; lateral fusiform gyri; and inferior temporal gyri, and in the ventral occipital cortex: posterior fusiform gyri; inferior occipital gyri; and mid-occipital gyri. Clusters of voxels that showed differential responses outside of these six regions included dorsal occipital cortex, and a region in the superior temporal sulcus. Figure 1 is a schematic illustration of these regions. Brain atlas coordinates for these regions are presented in Tables 2 and 3.

We first summarize our previous findings of differential activations in the ventral temporal cortex evoked by houses, faces, and chairs. We then compare these findings to differential patterns of activation seen in the ventral occipital regions, and contrast both with the pattern seen in the dorsal occipital cortex. Finally, we present data showing differential response to faces in the superior temporal sulcus.

Activation in the Ventral Temporal Cortex

In a recent paper, we identified, using fMRI, three bilateral regions in the ventral temporal cortex that consistently showed significantly different responses for houses, faces, and chairs (Ishai et al., 1999). Here, we summarize these earlier findings to facilitate comparison with our findings in the occipital cortex, which we report for the first time. Within ventral temporal cortex, a region in the medial portion of the fusiform gyrus, including the collateral sulcus, responded maximally to

Figure 1. Schematic illustration of the location of the ventral temporal and ventral occipital regions showing maximal responses to houses, faces, and chairs, shown on lateral and ventral views of the right hemisphere. Note that the full extent of the response to these object categories were distributed and overlapping (see Figure 5). A = dorsal occipital cortex; B = superior temporal sulcus; C = mid-occipital gyrus; D = inferior occipital gyrus; E = inferior temporal gyrus; F = lateral fusiform gyrus; G = posterior fusiform gyrus; H = medial fusiform gyrus.



houses. An adjacent region in the lateral fusiform gyrus and occipitotemporal sulcus responded maximally to faces. Lateral to this face-selective region, a region in the inferior temporal gyrus responded maximally to chairs. A small sector of the medial fusiform gyrus also responded most strongly to chairs. The medial-to-lateral topological arrangement of these regions was consistent across all subjects. Each object category evoked significant responses in the regions that responded maximally to other categories and was associated with a differential pattern of response in these other regions. For example, houses evoked a stronger response in the inferior temporal, chair-selective region than in the lateral fusiform, face-selective region (Figure 2). These results suggested that neural activity in

the regions that respond maximally to other categories carries information about the identity of nonpreferred categories.

The delayed matching task consistently evoked stronger responses than did passive viewing in all temporal regions ($p < .001$ in all cases). These tasks differ in terms of demands on attention as well as in the involvement of additional cognitive processes, such as working memory and, perhaps, mental rotation. The effect of increased cognitive demands on the response to houses and chairs was greater in the regions maximally responsive to the other nonface object (inferior temporal and medial fusiform gyri) than in the region maximally responsive to faces (lateral fusiform gyrus) ($p < .001$ in all cases). This differential effect of task

Table 2. Temporal and Occipital Regions Showing Differential Responses to Houses (H), Faces (F), and Chairs (C) in Experiment 1

<i>Region</i>	<i>Selectivity</i>	<i>Hemisphere</i>	<i>N</i>	<i>Volume (cm³) (mean ± SD)</i>	<i>x</i>	<i>y</i>	<i>z</i>
<i>Ventral occipital</i>							
Posterior fusiform gyri	H > F and C	left	6	2.2 ± 1.8	-22	-81	-18
		right	5	2.5 ± 0.7	26	-86	-14
Inferior occipital gyri	F > H and C	left	4	1.1 ± 0.5	-33	-79	-14
		right	4	1.4 ± 1.1	38	-82	-17
Mid-occipital gyri	C > F and H	left	5	4.2 ± 0.8	-37	-80	-7
		right	6	1.9 ± 0.8	43	-79	-1
<i>Ventral temporal</i>							
Medial fusiform gyri	H > F and C	left	6	3.8 ± 2.0	-26	-57	-14
		right	6	4.9 ± 2.9	28	-57	-13
Medial fusiform gyri	C > F and H	left	5	1.4 ± 0.8	-27	-51	-19
		right	4	1.1 ± 0.6	30	-49	-16
Lateral fusiform gyri	F > H and C	left	6	1.4 ± 0.6	-36	-55	-20
		right	6	1.7 ± 0.5	40	-52	-19
Inferior temporal gyri	C > F and H	left	6	1.4 ± 0.8	-41	-64	-12
		right	6	1.9 ± 0.7	48	-62	-11
<i>Other</i>							
Dorsal occipital	H > F and C	left	6	4.5 ± 1.9	-21	-84	23
		right	6	6.1 ± 4.0	29	-80	26
	C > F and H	left	6	3.7 ± 2.5	-21	-77	36
		right	5	1.4 ± 0.6	29	-80	35
Superior temporal sulci	F > H and C	left	3	1.7 ± 1.7	-53	-45	-4
		right	5	1.6 ± 1.3	54	-47	9
Intraparietal sulci	H > F and C	left	1	0.3	-32	-70	42
		right	2	1.1 ± 0.1	26	-58	45
	C > F and H	left	3	0.8 ± 0.4	-43	-50	49
		right	2	1.5 ± 0.5	34	-48	55

Volumes were calculated before spatial normalization. Coordinates are in the normalized space of the Talairach and Tournoux brain atlas (1988). *N* indicates number of subjects in whom each region was identified according to our criteria (seven or more contiguous voxels), and the mean for each region volume is calculated only for these subjects.

indicates that the regions maximally responsive to houses and chairs are recruited more to augment the perception of nonpreferred nonface objects than is the region maximally responsive to faces.

As shown in Figure 2, photographs and line drawings evoked the same pattern of differential responses, indicating that the differential activation was not due to some low-level features of the stimuli, such as spatial frequency or texture. Although the line drawings of houses, faces, and chairs clearly have different spatial frequencies, these spatial frequency differences are different from the spatial frequency differences among photographs of houses, faces, and chairs. If the different patterns of response to photographs were due to spatial frequency differences, then line drawings would have

produced a different set of differential patterns of response. We found, however, that the medial fusiform, lateral fusiform, and inferior temporal gyrus regions that responded most strongly to photographs of houses, faces, and chairs, respectively, also responded most strongly to line drawings of the same category ($p < .001$ in all cases).

Thus, these analyses indicated that the pattern of response to one stimulus category was not restricted to the region that responded maximally to that category but, rather, extended to the regions that responded maximally to other categories. Houses, faces, and chairs evoked distinct patterns of activation across a wide expanse of the ventral temporal cortex, suggesting that the functional architecture of this cortex contains a

Table 3. Temporal and Occipital Regions Showing Differential Responses to Houses (H), Faces (F), and Chairs (C) in Experiment 2

<i>Region</i>	<i>Selectivity</i>	<i>Hemisphere</i>	<i>N</i>	<i>Volume (cm³) (mean ± SD)</i>	<i>x</i>	<i>y</i>	<i>z</i>
<i>Ventral occipital</i>							
Posterior fusiform gyri	H > F and C	left	5	1.7 ± 1.1	-21	-87	-24
		right	4	1.6 ± 1.0	27	-88	-14
Inferior occipital gyri	F > H and C	left	5	1.0 ± 0.5	-34	-81	-25
		right	4	0.7 ± 0.3	41	-82	-15
Mid-occipital gyri	C > F and H	left	4	2.1 ± 0.3	-39	-84	-13
		right	4	1.8 ± 0.8	41	-90	1
<i>Ventral temporal</i>							
Medial fusiform gyri	H > F and C	left	6	2.7 ± 1.5	-25	-58	-16
		right	5	3.3 ± 1.1	28	-63	-18
Medial fusiform gyri	C > F and H	left	6	1.0 ± 0.6	-29	-56	-22
		right	3	0.9 ± 0.3	30	-61	-19
Lateral fusiform gyri	F > H and C	left	5	0.9 ± 0.5	-39	-64	-28
		right	5	1.9 ± 0.4	41	-60	-20
Inferior temporal gyri	C > F and H	left	6	1.3 ± 1.0	-42	-69	-14
		right	5	2.4 ± 0.7	48	-73	-8
<i>Other</i>							
Dorsal occipital	H > F and C	left	6	4.6 ± 2.4	-24	-80	34
		right	6	4.0 ± 2.4	29	-81	37
	C > F and H	left	6	1.9 ± 1.5	-26	-83	22
		right	5	1.2 ± 0.9	31	-79	36
Superior temporal sulci	F > H and C	left	2	0.6 ± 0.1	-53	-53	1
		right	6	1.2 ± 0.8	51	-59	18
Intraparietal sulci	H > F and C	left	1	1.6	-33	-54	57
		C > F and H	left	3	1.5 ± 1.5	-43	-48
	right		3	0.7 ± 0.3	33	-61	55

Volumes were calculated before spatial normalization. Coordinates are in the normalized space of the Talairach and Tournoux brain atlas (1988). *N* indicates number of subjects in whom each region was identified according to our criteria (seven or more contiguous voxels), and the mean for each region volume is calculated only for these subjects.

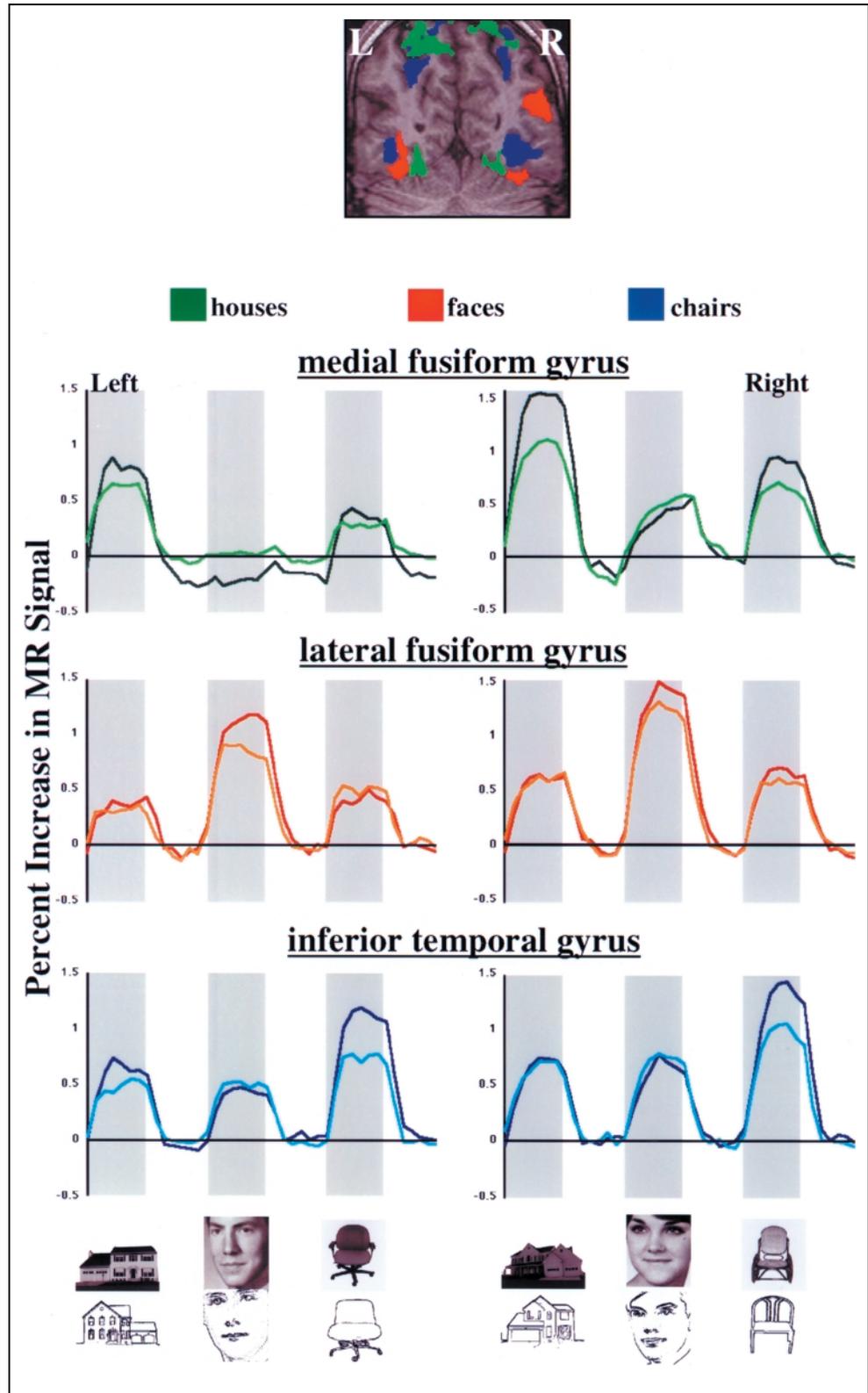
distributed representation of information about object form (Ishai et al., 1999).

Activation in the Ventral Occipital Cortex

The same differential pattern of activation seen in the ventral temporal cortex was found in the ventral occipital cortex (Tables 2 and 3). Thus, a medial region in the posterior fusiform gyrus and nearby occipital gyri responded most strongly to houses. Just lateral to this region, a region in the inferior occipital gyrus and inferior part of the mid-occipital gyrus responded most strongly to faces. Superior and lateral to this face-selective region was a region mainly in the mid-occipital gyrus that responded maximally to chairs. In most subjects, a division between the occipital and temporal regions

maximally responsive to faces could be discerned, separated by cortex showing less category selectivity. The divisions between the occipital and temporal regions maximally responsive to houses and chairs, on the other hand, were often less distinct. In these cases, the division between the temporal and occipital regions was set at the same coronal plane where the division between face-responsive regions was seen. After normalization to the Talairach and Tournoux brain atlas (1988), the mean coordinates (*N* = 12 subjects) for the anterior limit of the occipital category-selective regions and posterior limit of the temporal category-selective clusters were *y* = -74 mm (*SD* = 3.3) and *y* = -72 mm (*SD* = 4.6), respectively. As in the ventral temporal cortex, the medial-to-lateral topological arrangement of these ventral occipital regions was bilateral and consis-

Figure 2. Response topographies in ventral temporal cortex in Experiment 2. Top: Locations of three ventral temporal regions that responded differentially to houses, faces, and chairs, illustrated in a coronal section ($y = -66$) from a single subject. Voxels shown in color demonstrated a significant overall experimental effect ($Z > 4.0$) and a significant difference among responses to houses, faces, and chairs ($Z > 1.96$, clusters of seven or more voxels). Regions showing maximal responses to houses, faces, and chairs, are shown in green, red, and blue, respectively. Bottom: Mean time series for these three ventral temporal regions. Data are averaged across six subjects and six repetitions of task blocks in each subject. Gray bars indicate presentation of meaningful stimuli. The white space to the right of each gray bar indicates the presentation of control stimuli. The darker colored line in each graph is for the delayed match-to-sample task with photographs, and the lighter line is for delayed matching with line drawings. These data were presented in a different format in a recent paper (Ishai et al., 1999) and are shown here for direct comparison with the data presented in Figure 3.



tent across subjects (see Tables 2 and 3 for mean coordinates).

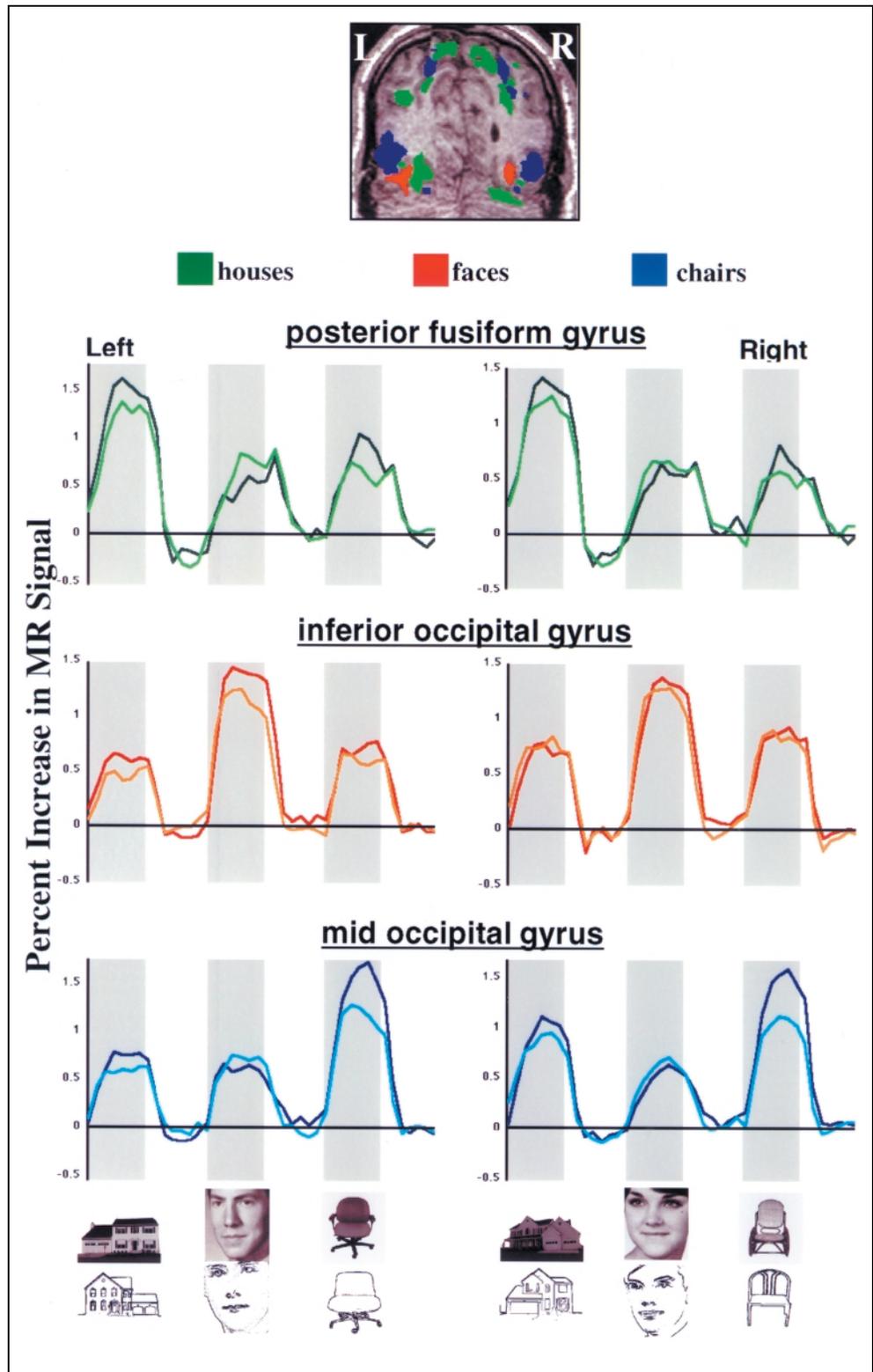
Although each of the ventral occipital regions responded maximally to one object category, the nonpre-

ferred categories also evoked significant activations. For example, the maximal response to houses was in the posterior fusiform gyrus, but significant responses were also observed in the more lateral inferior and mid-

occipital regions that responded maximally to faces and chairs, respectively. Similarly, significant activations to nonpreferred categories were found outside the regions that responded maximally to faces and chairs (Figures 3 and 4). Thus, as in the ventral temporal cortex, the

response to a category of objects in the ventral occipital cortex was not restricted to a single region that responded maximally to that category but rather showed a distributed pattern of response across a broad expanse of cortex. To emphasize the distributed nature of the

Figure 3. Response topographies in ventral occipital cortex in Experiment 2. Top: Locations of three ventral occipital regions that responded differentially to houses, faces, and chairs, illustrated in a coronal section ($y = -78$) from a single subject. Bottom: Mean time series. The darker colored line in each graph is for the delayed match-to-sample task with photographs, and the lighter line is for delayed matching with line drawings.

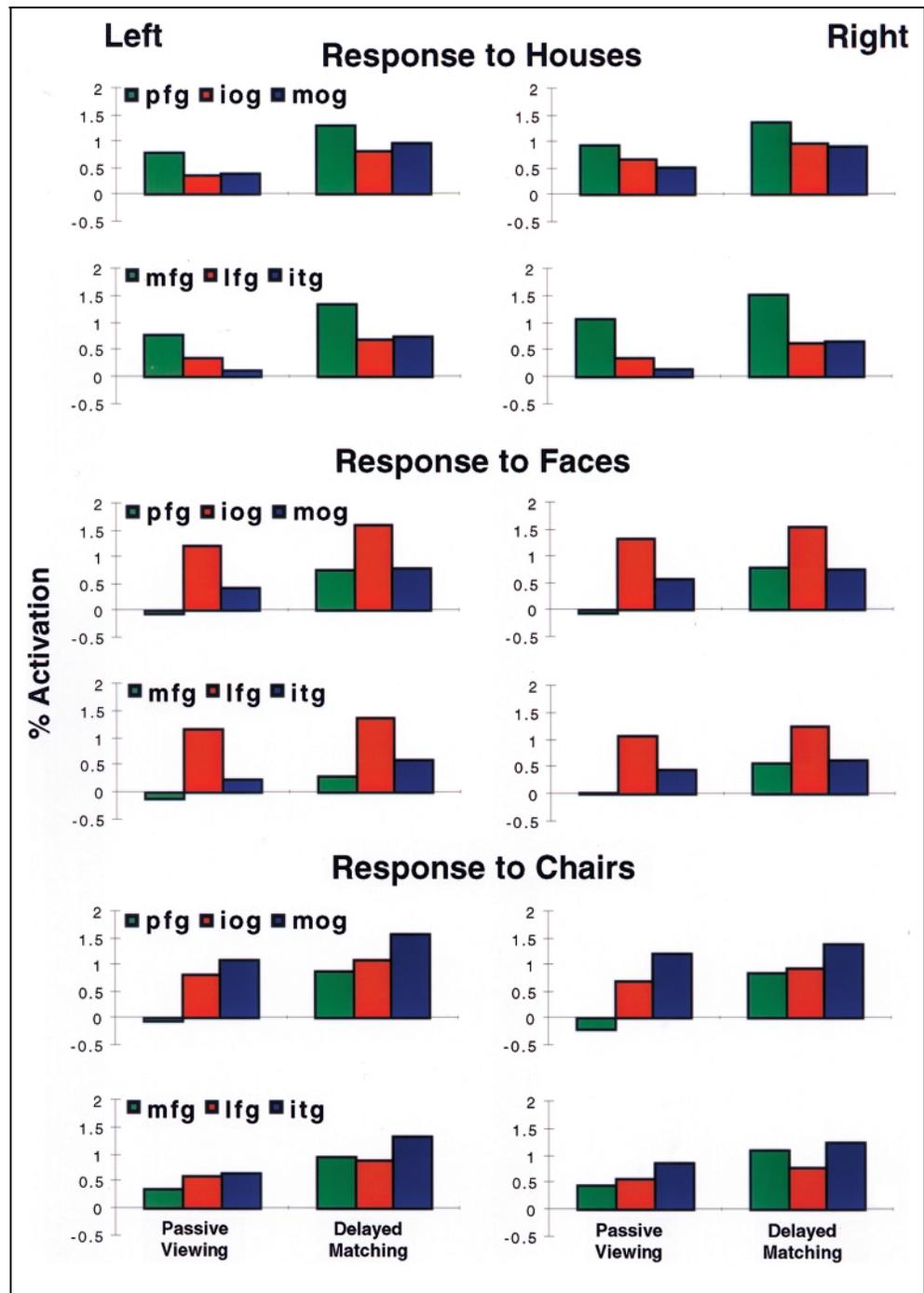


response evoked by each object category, we examined the response evoked by a category relative to the scrambled pictures baseline across all regions, rather than the differential responses to categories within each region (Figures 2 and 3). As illustrated for a single subject in Figure 5, it is clear that in all the ventral occipital and ventral temporal regions the response was

not restricted to the region that responded maximally to that category but, rather, extended to adjacent regions that responded maximally to other categories as well as to the cortex in between category-selective regions (shown in white).

Performance of the delayed matching task, as compared to passive viewing, consistently evoked a stronger

Figure 4. Patterns of response to houses, faces, and chairs across regions in ventral occipital (top) and ventral temporal (bottom) cortex. Results from Experiments 1 are shown in the same graphs to allow direct comparison of the patterns of response during passive viewing and delayed matching tasks. Occipital regions: PFG = posterior fusiform gyrus; IOG = inferior occipital gyrus; MOG = mid-occipital gyrus. Temporal regions: MFG = medial fusiform gyrus; LFG = lateral fusiform gyrus; ITG = inferior temporal gyrus.



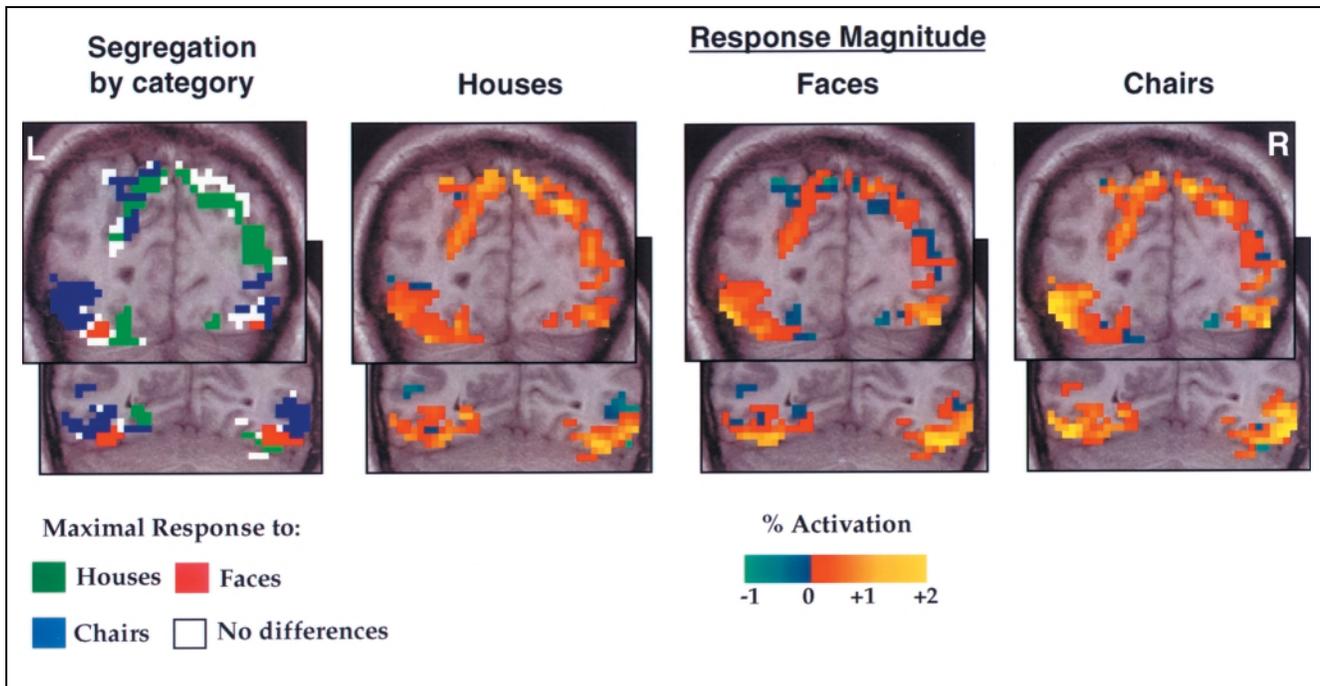


Figure 5. Distributed patterns of response to houses, faces, and chairs in two coronal sections through ventral temporal and ventral occipital cortex in one subject. Regions showing maximal responses to houses, faces, and chairs are shown in green, red, and blue, respectively. White voxels indicate significant activation across stimulus categories, but no significant differences among categories. Strength of response to houses, faces, and chairs, relative to control tasks with scrambled pictures, is shown in all ventral temporal voxels that showed a significant experimental effect ($Z > 4.0$). Talairach coordinates: Top row: $y = -86$; Bottom row: $y = -66$.

response for all categories ($p < .001$ in all regions, Figure 4). As in the ventral temporal cortex, the responses to the two nonface object categories were augmented more in the ventral occipital region that responded maximally to the other nonface category than in the ventral occipital region that responded maximally to faces ($p < .001$ for chairs on the left and right, $p < .05$ for houses on the left only).

We had shown that the differential patterns of response to houses, faces, and chairs in the ventral temporal cortex were probably not due to low-level visual features, such as spatial frequency and texture, by demonstrating that the patterns of differential responses evoked by photographs were similar to the patterns evoked by line drawings during delayed matching. However, it remained a possibility that, in the more posterior ventral occipital regions, line drawings and photographs would evoke different patterns of response because the responses in these regions may be more dependent on simpler visual features. This was not the case, however, as shown in Figure 3. The three ventral occipital regions that responded most strongly to photographs of a given category of objects also responded maximally to line drawings of the same category ($p < .001$ in all cases). For example, the posterior fusiform gyrus region responded maximally to both photographs and line drawings of houses.

Comparison of the Ventral Temporal and Ventral Occipital Regions

The distributed category-related patterns of response across ventral temporal and ventral occipital regions were remarkably similar (see Figures 2, 3, and 4). The single exception appeared to be the absence of a response to chairs during passive viewing in the posterior fusiform gyrus within occipital cortex and the presence of a response in the medial fusiform gyrus within temporal cortex. However, during delayed matching, the response to chairs in these regions was very similar for Experiments 1 and 2.

In order to determine if category selectivity was greater in the temporal than in the occipital cortex, we compared the responses to the preferred categories to the responses to the nonpreferred categories in each category-selective region of cortex. On average, the amplitude of responses to preferred categories were 1.4% greater than baseline in the occipital cortex and 1.3% greater than baseline in the temporal cortex. The amplitude of responses to nonpreferred categories were 0.8% greater than baseline in the occipital cortex and 0.6% greater than baseline in the temporal cortex. The slight decrease in response magnitude in the temporal as compared to the occipital cortex was significant ($p < .01$ for houses, $p < .001$ for faces and chairs), but the slight

increase in selectivity was significant only for the houses ($p < .01$). These results suggest only a weak trend towards greater category-selectivity in the ventral temporal as compared to the ventral occipital cortex.

Activation in the Dorsal Occipital Cortex

In both experiments, regions in the dorsal occipital cortex were found that responded maximally to houses and chairs (Figure 6, Tables 2 and 3). Interestingly, no voxels were found that responded maximally to faces. Moreover, during passive viewing the response to faces in the house- and chair-selective voxels in the dorsal occipital cortex was negligible (Figure 6A). Across subjects, there did not appear to be any consistent pattern in the location of the clusters of voxels maximally responsive to houses relative to those maximally responsive to chairs. Rather, clusters of voxels maximally

responsive to houses were intermixed with those maximally responsive to chairs.

In Experiment 1, relative to passive viewing, the delayed matching task increased the responses in the dorsal occipital regions. The increase in the responses, during delayed matching, however, was not uniform across all object categories. In voxels that responded maximally to houses, the increase in the cognitive demand had a greater effect on the response to chairs than on the response to faces (1.12 vs. 0.84% on the left, 1.14 vs. 0.78% on the right, $p < .005$ in both cases). Similarly, in the voxels that responded maximally to chairs, the effect of increased cognitive demand was greater on the response to houses than to faces (1.12 vs. 0.71% on the left, 0.99 vs. 0.61% on the right, $p < .001$ in both cases). It therefore appears that in the dorsal occipital cortex, as in the ventral temporal and ventral occipital cortex, the regions maximally responsive to houses are preferentially recruited to augment the

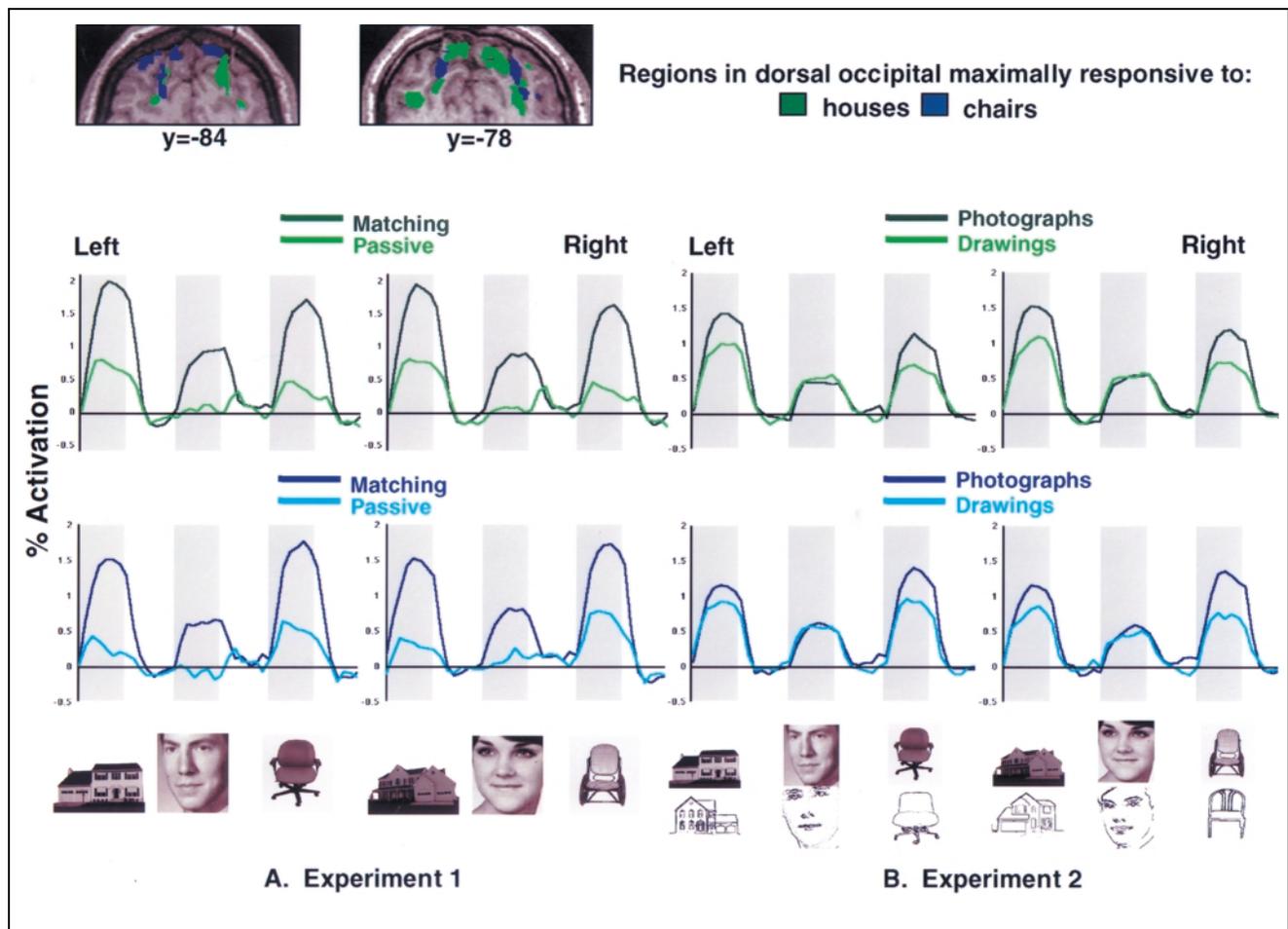


Figure 6. Response topographies in dorsal occipital cortex. Top: Locations of clusters that responded maximally to houses and chairs, illustrated in two coronal sections from two subjects ($y = -84$ and $y = -78$, respectively). Regions showing maximal responses to houses and chairs are shown in green and blue, respectively. Note that voxels that respond maximally to faces were not found. Bottom: (A) Patterns of response to houses and chairs in dorsal occipital cortex in Experiment 1. The darker colored line in each graph is for the delayed match-to-sample task, and the lighter line is for the passive viewing task. (B) Patterns of response to houses and chairs in dorsal occipital cortex in Experiment 2. The darker colored line in each graph is for the delayed match-to-sample task with photographs, and the lighter line is for delayed matching with line drawings.

perception of chairs, and conversely, that the regions maximally responsive to chairs are preferentially recruited to augment the perception of houses.

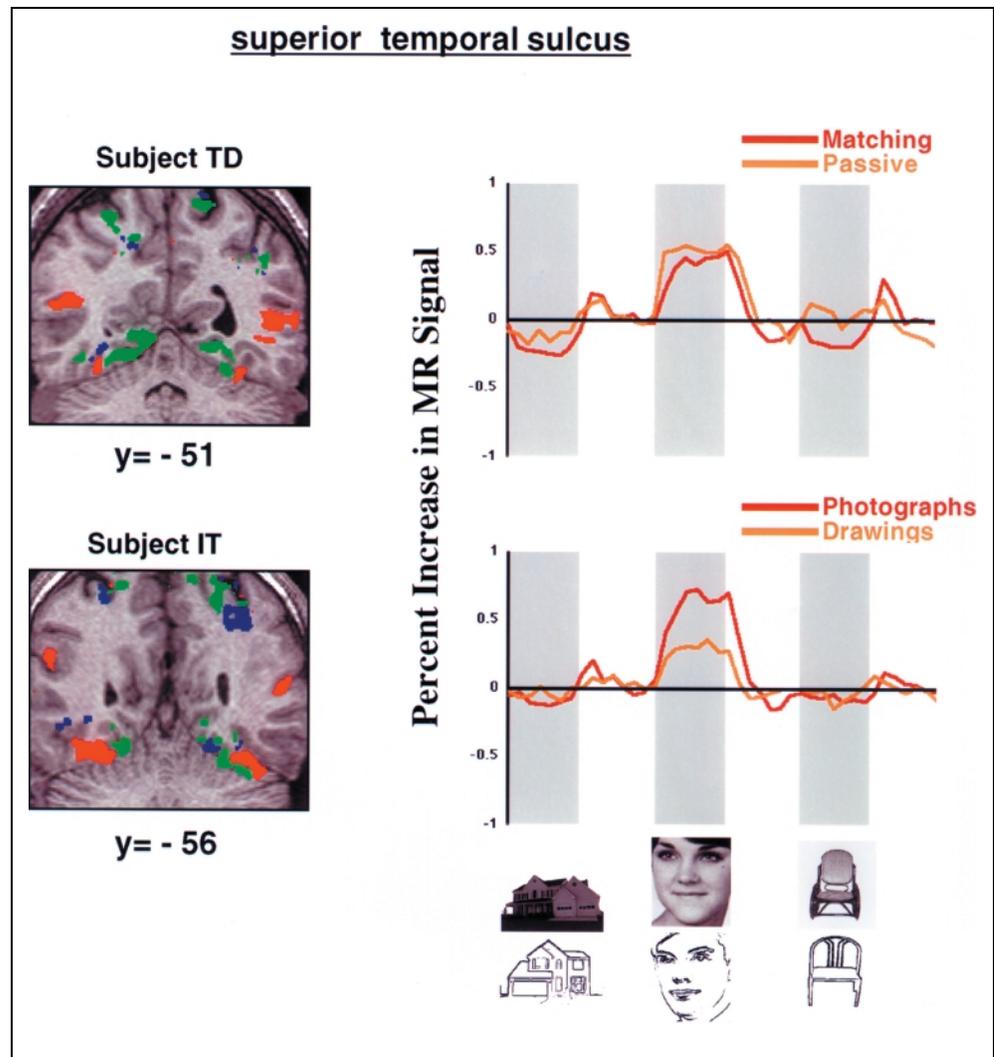
In Experiment 2, the dorsal occipital regions that responded maximally to photographs of houses also responded maximally to line drawings of houses ($p < .001$ in both hemispheres). Similarly, the dorsal occipital regions that responded maximally to photographs of chairs also responded maximally to line drawings of chairs ($p < .001$ on the left, $p < .01$ on the right). In this respect, these dorsal occipital regions resembled both the ventral temporal and ventral occipital regions (cf. Figures 2, 3, and 6).

The dorsal occipital regions could be distinguished from both ventral temporal and ventral occipital regions not only by the absence of a face-selective response but also by an enhanced general effect of increased cognitive demands. When we compared passive and matching tasks in the house- and chair-selective regions of the dorsal occipital with the house- and chair-selective regions of the ventral occipital and

ventral temporal, we found that the increased cognitive demands had a greater effect on the response to houses in the house-selective dorsal occipital region (1.1%) than in both the house-selective posterior fusiform region (0.48%) ($p < .001$ in both hemispheres) and in the house-selective medial fusiform region (0.5%) ($p < .001$ in both hemispheres). Similarly, the effect of increased cognitive demands on the response to chairs (1.0%) was greater in the chair-selective dorsal occipital region than in both the chair-selective mid-occipital region (0.35%) ($p < .001$ in both hemispheres) and the chair-selective inferior temporal region (0.53%) ($p < .001$ in both hemispheres). Thus, the effects of increased cognitive demands in the house- and chair-selective dorsal occipital regions were greater than in the regions of the ventral occipital and ventral temporal cortex that responded maximally to these same categories.

In both Experiments 1 and 2, activation was also seen in the intraparietal sulcus (IPS). Like dorsal occipital regions, clusters of voxels in the IPS responded maxi-

Figure 7. Responses in superior temporal sulcus to houses, faces, and chairs. Mean time series are shown for the right hemisphere ($N = 5$ in Experiment 1, $N = 6$ in Experiment 2).



mally to houses and chairs, but not to faces. As only a few subjects showed category-related differences in their IPS responses, data from these regions were not analyzed further (see Table 2 and 3).

Differences Between Face and Object Perception

Although the representations of faces and other objects overlap in both the ventral temporal and ventral occipital cortex, the data indicate that the representation of faces is more restricted in the spatial extent and is activated more automatically than are the representations of houses and chairs. Of the voxels in the ventral temporal cortex that demonstrated category selectivity, 46% responded maximally to houses, 36% responded maximally to chairs, and 18% responded maximally to faces. Similarly, of the voxels in the ventral occipital cortex that demonstrated category selectivity, 36% responded maximally to houses, 45% responded maximally to chairs, and 19% responded maximally to faces. The differences between the volumes of face-, house-, and chair-selective clusters in both experiments across ventral temporal and ventral occipital cortices were significant ($p < .01$ in both hemispheres). Additionally, whereas regions were identified in the dorsal occipital cortex that responded maximally to houses and chairs, none responded maximally to faces. Faces, therefore, appear to be special insofar as their representation is more restricted to ventral extrastriate cortex and is not as widely distributed there, as compared to the representations of other objects.

A region in the superior temporal sulcus was identified that seemed to respond almost exclusively to faces, unlike the face-responsive regions in the ventral occipital and temporal cortex that also responded significantly to other categories. This small superior temporal region, seen in most subjects ($N = 11$ on the right, $N = 5$ on the left), responded more to faces than to houses or chairs (Figure 7, Tables 2 and 3). Indeed, the response to both houses and chairs was negligible in this region, during both passive viewing and matching. Moreover, passive viewing of faces gave as robust a response as matching faces, suggesting a special status for face processing within this region.

Increased cognitive demands did have an effect on face-selective regions in the ventral temporal and ventral occipital cortex, but less so than the effects in the house- and chair-selective regions. Relative to the passive viewing task, performance of the matching task resulted in an increase in activation of 49% to houses in the house-selective regions of the ventral temporal and ventral occipital cortex, an increase of 44% to chairs in the chair-selective regions, but a significantly smaller increase of only 25% to faces in the face-selective regions ($p < .001$ for both comparisons), suggesting that face perception is more automatic.

DISCUSSION

In the present study, we investigated whether regions of occipital cortex, like those of the ventral temporal cortex, would show evidence of category-related patterns of response to houses, faces, and chairs. The results demonstrated differential responses to these categories of objects in both the ventral and dorsal occipital cortex. The results also demonstrated a face-specific response in a small region of the superior temporal sulcus. Within all regions of occipital and temporal cortex showing preferential responses, the differential pattern of activation evoked by each category of objects was similar for different tasks (passive viewing or delayed matching) and stimulus types (photographs or line drawings).

Our current findings indicate that the topological arrangement of category-selective regions in the ventral occipital cortex is remarkably similar to the topological arrangement in the ventral temporal cortex that we reported earlier (Ishai et al., 1999). We found a medial house-selective region in the posterior fusiform gyrus, a face-selective region lateral to it in the inferior occipital gyrus, and a more laterally and superiorly located chair-selective region in the mid-occipital gyrus. As in the ventral temporal cortex, the response to each category in the ventral occipital cortex was not restricted to the region that responded maximally to that category. The ventrolateral occipital face- and chair-selective clusters are located in the posterior section of the LO complex (Grill-Spector et al., 1999), a region that was originally defined based on its greater response to assorted objects than to texture patterns (Malach et al., 1995). Our results, therefore, indicate that objects evoke category-related patterns of response in the LO as well as in the ventral temporal cortex. Occipital face- and house-selective regions have been reported previously (Halgren et al. 1999; Haxby et al. 1999; Kanwisher et al. 1997), but it was unclear if the occipital regions showed the same degree of category-selectivity as seen in the ventral temporal cortex. Our data showed only scant evidence for an increase in specificity in the regions of the ventral temporal cortex compared to either ventral occipital or dorsal occipital cortex, in terms of the differential response to the preferred and nonpreferred categories. Our results, therefore, suggest that segregation of the perceptual representations of objects by features that distinguish categories may occur as early as in the occipital extrastriate cortex. Alternatively, the differential patterns of response in the occipital cortex could reflect top-down modulation of these regions by the ventral temporal cortex.

Category-related patterns of response were also found in the regions of the dorsal occipital cortex. Whereas category-related responses in both the ventral temporal and ventral occipital cortex exhibited a consistent topological arrangement, no such topology was found in the

dorsal occipital cortex. Clusters of voxels maximally responsive to houses or chairs were intermixed. The absence of a consistent topological arrangement of activated regions in the dorsal occipital cortex suggests a different functional architecture from that proposed for the ventral temporal and ventral occipital cortex. One interesting possibility is that the representations of nonface objects are more parts-based, perhaps because the spatial arrangements of the parts of nonface objects are more variable. For example, the arrangement of the windows, door, and garage in a house is more variable than is the arrangement of the eyes, nose, and mouth in a face, and the representation of a house may, therefore, require a more explicit representation of this spatial arrangement. The category-selective activity in the dorsal occipital regions may represent this spatial information, and is consistent with the participation of the dorsal occipital cortex in spatial perception (Haxby et al., 1994).

The similarity between the patterns of category-related responses to photographs and line drawings suggests that these patterns are not attributable to different spatial frequencies. Although line drawings of faces, houses, and chairs also have differences in the spatial frequencies, the differences are not the same as the spatial frequency differences for photographs of these categories. Nonetheless, spatial frequency as a possible explanation for these differential responses could be more definitively ruled out by an experiment with house, face, and chair stimuli that have been filtered to match spatial frequencies.

The response to each object category was not restricted to those occipital and temporal regions that responded maximally to that category. Moreover, the response to nonpreferred objects in a category-related region appeared to carry information about the identity of those objects, as indicated both by differential responses to nonpreferred categories (Ishai et al., 1999) and by differential effects of increased cognitive demands on the responses to nonpreferred categories. The distributed nature of the response to houses, faces, and chairs reported here suggests that the representations of faces and objects are not restricted to patches of cortex that respond exclusively to one category but, rather, are broad and overlapping. The ventral temporal “face-” and “house-selective” regions identified in our study were larger compared to other reports (e.g., Aguirre et al., 1998; Kanwisher et al., 1997). We deliberately used less stringent statistical criteria to identify these regions, so that we could analyze the full extent of cortex that demonstrates category-related patterns of response. Nonetheless, the selectivity of the response within these regions (in terms of the amplitude of the response to the preferred category as compared to the nonpreferred categories) was comparable to the selectivity reported by the aforementioned studies. During passive viewing, the response to faces in the ventral

temporal region that responded maximally to houses was nil, and the response to houses in the ventral temporal region that responded maximally to faces was one-third of the response to faces.

Based on our findings, we propose the object form topology hypothesis, according to which the functional architecture of the neural systems for face and object perception is based on a distributed representation of attributes of object form, such that attributes that are shared by members of a category cluster together. The responses to different object categories in this system are distributed and overlapping but are nevertheless distinct by virtue of differential patterns of response strength. This representation has a topological arrangement that is consistent across subjects. The nature of these attributes is unknown, but may consist of object primitives similar to those proposed in Tanaka’s (1993, 1996) studies of the monkey inferior temporal cortex. While a category-specific modular organization could never provide a comprehensive account for the perception of all categories (as there are too many categories and too little cortex), a distributed representation of attributes of object form could produce an unlimited variety of patterns of response for different categories, and is consistent with monkey physiology (cf. Tanaka 1993, 1996) and computational models of object recognition (Wallis & Bulthoff, 1999; Edelman, Grill-Spector, Kushnir, & Malach, 1998; McClelland & Rumelhart, 1985). Nonetheless, within this distributed representation for object form, some classes of stimuli may have a special status, the best candidate being faces (Tovee, 1998; Moscovitch, Wincour, & Behrmann, 1997; Farah, 1996). Electrophysiological studies have reported face-specific ERPs that were localized to patches in the ventral occipitotemporal cortex (Puce et al., 1999; Allison et al., 1994). The existence of face-specific cortical sites suggests that within the broader regions we have identified there are small patches of cortex that respond exclusively to one category. These findings can be integrated into a “mixed model,” according to which object representation “units” are embedded within the large cortical regions that respond to attributes of object form. Nonetheless, the existence of face-selective sites does not resolve the question of whether these regions represent attributes of object form that are associated exclusively with a category, or have a higher-order role as “object representation units” that use input from surrounding cortex to identify faces.

Our results demonstrate several differences between the neural representations of faces and other objects. Faces may be special insofar as their representation is more restricted than are the representations of other objects; as reflected by the volume of the face-responsive regions, as compared to the house- and chair-responsive regions, as well as by the weaker responses to faces, as compared to the response to chairs, in the house-responsive regions. This restricted representa-

tion of faces may explain prosopagnosia, the inability to recognize familiar faces (Behrman, Winocur, & Moscovitch, 1992; Damasio, Tranel, & Damasio, 1990; Damasio, Damasio, & Van Hoesen, 1982; Whately & Warrington, 1977). A lesion in the ventral occipitotemporal cortex would be more likely to encompass all of the cortex responding to faces than all of the cortex responding to nonface objects. Additionally, the response to faces seems more automatic, as suggested by the smaller effect of increased cognitive demands. These differences, however, may not reflect the existence of a special neural system dedicated to face perception but, rather, may be accounted for by subjects' greater expertise at face perception (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999), or by the smaller range of visual differences among faces as compared to the allowable ranges of differences for houses and chairs. The special status of the neural system for faces is called further into question by our recent finding that the pattern of response to animals has its peak in the same temporal and occipital regions that respond maximally to faces, even when the animals' faces are obscured (Chao, Haxby, et al. 1999, Chao, Martin, & Haxby, 1999), suggesting that these regions also may be maximally responsive to nonfacial aspects of animal form.

The most selective response to faces was observed in the superior temporal sulcus. Other studies have shown activation in a similar location evoked by the perception of faces (Chao, Haxby, et al., 1999; Halgren et al. 1999; Haxby et al. 1999; Kanwisher et al. 1997), by the perception of eye and mouth movement (Puce et al., 1996), and gaze direction (Hoffman & Haxby, 2000). This region may be the human homologue of the region on the upper bank of the superior temporal sulcus in the monkey that contains a high percentage of face-selective neurons, many of which are sensitive to the direction of eye gaze and the angle of profile (Rolls, 1992; Perrett, Rolls, & Caan, 1982). However, the perception of hand and body movement (Bonda, Petrides, Ostry, & Evans, 1996), as well as photographs of animals, but not tools, evoke a response in this region (Chao, Haxby, et al., 1999). This suggests that the superior temporal sulcus plays a more general role in the perception of biological movement and the perception of static configurations of the face and body that are achieved by movement.

Thus, we found that different categories of objects evoke distinct patterns of response in the ventral occipital cortex that have a topology that is similar to that found in the ventral temporal cortex. Moreover, the selectivity of category-related responses were equivalent for ventral occipital and ventral temporal cortex. This surprising finding may reflect a top-down influence on these occipital regions, but it is also possible that category-related visual attributes are segregated at this earlier stage. Information about the

temporal dynamics of category-related responses in the occipital and temporal cortex may help to distinguish these possibilities. Category-related patterns of response were not restricted to ventral extrastriate cortex but were also found in the dorsal occipital and superior temporal sulcal cortex. In addition, the representation of faces differed more from the representations of houses and chairs than the representations of houses and chairs differed from each other, but it is still unclear whether the representations of faces and nonface objects are better thought of as separate neural systems or as a more general system that can represent both faces and nonface objects with overlapping but distinct patterns of response. Our results indicate that the representations of faces and objects in the ventral visual pathway have a topological organization that is remarkably consistent across subjects, suggesting that it does not develop idiosyncratically but, rather, that it develops according to principles of organization that are common across individuals. The nature of these principles of organization is unknown, but they are evident in a neural architecture that exists at a spatial scale that can be investigated with functional brain imaging.

METHODS

Subjects

Twelve normal, right-handed subjects (six males, six females, age 26 ± 3 years), with normal vision, participated in this study. Six subjects participated in Experiment 1 and the other six participated in Experiment 2. 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, Parasuraman, Lalonde, & Abboud, 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. In Experiment 1, subjects were presented with gray-scale photographs of houses, faces, and chairs. In Experiment 2, both gray-scale photographs and black and white line drawings were used. Line drawings of houses, faces, and chairs were obtained by converting the original gray-scale photographs in version 4.0 of Adobe Photoshop for Power Macintosh (Adobe Systems, San Jose, CA). The control stimuli for both photographs and line drawings were phased scrambled pictures (retaining spatial frequency information) of those stimuli. All stimuli were presented in the center of the screen on a gray background.

Experimental Procedure

In Experiment 1, subjects performed passive viewing and delayed match-to-sample tasks. In the passive viewing task, single stimuli (houses, faces, chairs, and scrambled pictures) were presented at a rate of 2/sec. In the delayed matching task, a single sample stimulus (presented for 1.5 sec) was followed, after a 0.5-sec delay, by a pair of choice stimuli (presented for 2 sec). The sample and matching choice stimuli were photographs of the same house, face, or chair taken from different viewing angles. Subjects indicated which choice stimulus matched the sample by pressing a button with the right or left thumb, and reaction time was recorded. The results of a psychophysical pilot experiment indicated that the house-, face-, and chair-matching tasks were equated for difficulty, in terms of reaction time and accuracy. These results were confirmed in the imaging experiments (see Results). In the control task, which controlled for both visual stimulation and motor response, scrambled pictures were presented with the same timing as the object pictures, and subjects responded by pressing both right and left buttons simultaneously. Before the scanning session, subjects were pretrained with the delayed match-to-sample task. The short practice session consisted of five trials of each object category, with stimuli that were not used in the experiment. Alternating runs of six matching and six passive viewing time series were obtained for each subject. Within a run, each 21-sec block with one visual category (houses, faces, chairs) was followed by a 21-sec control block with scrambled pictures of objects in that category. The order of category blocks was counterbalanced across runs. Each category and its scrambled pictures appeared twice in each time series. Across subjects, the order of passive viewing and matching time series was counterbalanced.

In Experiment 2, subjects performed the delayed match-to-sample task with photographs and line drawings of houses, faces, and chairs. The photographic sample and choice stimuli were taken from different viewing angles, as in Experiment 1, while the line drawings of sample and choice stimuli were presented at the same viewing angle. Each scan session consisted of six matching time series with photographs and six time series with line drawings, with the same counterbalancing as in Experiment 1.

Data Acquisition

A 1.5-T General Electric Signa scanner with whole head RFD coil was used. Changes in the blood oxygen level-dependent T2*-weighted MRI signal were measured using a gradient-echo echoplanar sequence (TR = 3 sec, TE = 40 msec, FOV = 20 cm, 64 × 64 matrix, voxel size = 3.125 × 3.125 × 5 mm). In each time series, 18 contiguous, 5-mm thick coronal slices were obtained.

High-resolution spoiled gradient recalled echo structural images were also acquired at the same locations as the echo-planar images (28, 5-mm thick coronal slices, TR = 13.9 msec, TE = 5.3 msec, FOV = 20 cm, 256 × 256 matrix). In a separate session, high-resolution full volume structural images were obtained for all subjects, using fast SPGR imaging (124, 1.5-mm thick sagittal slices, TR = 13.9, TE = 5.3, FOV = 24 cm, 256 × 256 matrix). These T1-weighted images provided detailed anatomical information for registration and 3D normalization to the Talairach and Tournoux atlas (1988).

Data Analysis

FMRI scan volumes were registered with an iterative method (Woods, Cherry, & Mazziotta, 1992), spatially smoothed in-plane with a Gaussian filter (full-width at half-maximum of the Gaussian distribution was 3.75 mm along the x and y axis), and ratio-normalized to the same global mean intensity. The hemodynamic response was modeled as a Gaussian curve with a mean equal to the estimated lag of 4.8 sec, and with a standard deviation equal to the estimated temporal dispersion of 1.8 sec (Maisog, Clark, Courtney, & Haxby, 1995).

The responses to the different object categories were analyzed using multiple regression (Haxby, Maisog, & Courtney, 2000; Friston et al., 1995), with regressors related to three orthogonal contrasts. Three complementary models were used. The first model was based on the dual system hypothesis that the recognition of faces and the recognition of other objects are mediated by different mechanisms in the ventral object vision pathway. The three orthogonal contrasts were as follows: meaningful objects versus control stimuli, faces versus houses and chairs, and houses versus chairs. The other two models tested different orthogonal contrasts (meaningful objects vs. control stimuli, houses vs. faces and chairs, and faces vs. chairs; meaningful objects vs. control stimuli, chairs vs. faces and houses, and faces vs. houses). All three models yield identical estimates for the sizes of activation for each category and identical results for the omnibus test of significant differences among the three categories, namely the combined effect of the second and third regressors. Waveforms representing the three effects of interest were then convolved with a model of the hemodynamic response to generate expected responses. Effects of no interest, such as run-to-run changes in the mean intensity and in the within-run linear trends, were included in the linear model. Extra sums of squares were used to form a statistical test, Wilks' Λ , for hypothesis testing. The Wilks' Λ maps were converted into F test maps, which were in turn converted into Z score maps.

To identify the brain regions that responded differentially to the visual presentation of houses, faces, and chairs, voxels were selected that showed a significant experimental effect ($Z > 4$, $p < .00004$) for the com-

bined effect of the three regressors of interest in the analysis of all 12 time series, an overall increase in activity for meaningful stimuli (a positive regression weight for the contrast between meaningful and control stimuli), and a significant differential category effect ($Z > 1.96, p < .025$, for the combined effect of the second and third regressors) in the combined analysis of matching and passive time series in Experiment 1 (12 time series) or in the analysis of the photographs condition in Experiment 2 (6 time series). Voxels were then segregated into clusters according to the category of objects that evoked the maximal response. Clusters of seven or more contiguous voxels were considered significant. A cluster of this size had a statistical significance of $p < .05$ in each subject.

For each subject and each region, a mean time series averaged across voxels in the region and across repetitions of blocks with the same object category was calculated. Means for the control blocks following each type of object category were also calculated. These mean time series consisted of 42 time points (7 time points for each object category and 7 time points for each control block). Each time point in the mean time series represents the average of 12 scans. For each subject, the size of the response to each object category in each region was estimated using multiple regression, with different regressors modeling the response to each category. These estimates of response magnitude were converted to percent changes above control task baseline and analyzed with four-way repeated measures ANOVAs (task \times hemisphere \times region \times stimulus category) with planned comparisons for selected contrasts. Separate ANOVAs analyzed the effect of task (matching vs. passive viewing tasks, Experiment 1), the replication of the matching with photographic stimuli (Experiments 1 and 2), and the effect of changing low-level visual features (photographs vs. line drawings, Experiment 2).

The anatomical locations of clusters of voxels showing significant differences between responses to houses, faces, and chairs were determined by superimposing the statistical maps on coplanar high-resolution structural images. The partial volume structural images were registered with the full volume high-resolution images using Automated Image Registration (Woods, Mazziotta, & Cherry, 1993). The full volume high-resolution images were normalized to the Talairach and Tournoux atlas (1988) using SPM96. Both transformations (registration and normalization) were then applied to the statistical maps, in order to obtain the Talairach coordinates of brain regions that responded maximally to houses, faces, and chairs.

Acknowledgments

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The data reported in this experiment have been deposited in National fMRI Data Center (<http://www.fmridc.org>). The accession number is 2-2000-1113D.

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