

Distributed Neural Systems for the Generation of Visual Images

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Summary

Visual perception of houses, faces, and chairs evoke differential responses in ventral temporal cortex. Using fMRI, we compared activations evoked by perception and imagery of these object categories. We found content-related activation during imagery in extrastriate cortex, but this activity was restricted to small subsets of the regions that showed category-related activation during perception. Within ventral temporal cortex, activation during imagery evoked stronger responses on the left whereas perception evoked stronger responses on the right. Additionally, visual imagery evoked activity in parietal and frontal cortex, but this activity was not content related. These results suggest that content-related activation during imagery in visual extrastriate cortex may be implemented by “top-down” mechanisms in parietal and frontal cortex that mediate the retrieval of face and object representations from long-term memory and their maintenance through visual imagery.

Introduction

Visual imagery is the ability to generate percept-like images in the absence of retinal input. The subjective similarity of seeing and imagining suggests that perception and imagery share common internal representations. 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; Goldensberg et al., 1989; Ishai and Sagi, 1995, 1997a, 1997b). Numerous neuroimaging studies have shown that visual imagery, like visual perception, evokes activation in occipitoparietal and occipitotemporal visual association areas (Roland and Gulyas, 1994; Mellet et al., 1996, 1998; D’Esposito et al., 1997). In some studies, the primary visual cortex (Le Bihan et al., 1993; Kosslyn et al., 1993, 1995a, 1999) and the lateral geniculate nucleus (Chen et al., 1998) were found to be activated during visual imagery, suggesting that the generation of mental images may involve sensory representations at the earlier processing stages in the visual pathway.

Studies of patients with brain damage have demonstrated a dissociation of visual-object and visual-spatial imagery (Levine et al., 1985), indicating that different

parts of the visual system mediate imagery for different types of visual information. Patients with prosopagnosia due to occipitotemporal damage were unable to imagine objects, but their spatial imagery was intact, whereas patients with visual disorientation due to occipitoparietal damage had impaired visual-spatial imagery but were able to imagine objects. Thus, the dissociation of “what” and “where” in imagery disorders parallels the two anatomically distinct visual systems proposed for visual perception (Ungerleider and Mishkin, 1982).

Recently, we and others have shown that within the ventral object vision pathway, faces and other objects, such as outdoor scenes, houses, chairs, animals, and tools, have distinct representations that can be dissociated with functional brain imaging (Kanwisher et al., 1997; McCarthy et al., 1997; Epstein and Kanwisher, 1998; Aguirre et al., 1998; Chao et al., 1999; Gauthier et al., 1999; Haxby et al., 1999; Ishai et al., 1999; Puce et al., 1999). In particular, we have shown that houses, faces, and chairs evoked maximal responses in distinct occipital and ventral temporal regions, and these regions have a topological arrangement that is consistent across subjects (Ishai et al., 1999, 2000). We decided to investigate whether visual imagery of these object categories evokes content-related patterns of response within the same regions of the ventral object vision pathway. Additionally, we asked whether other parts of the brain were activated by imagery that might provide the input or control signal to visual extrastriate cortex that generates percept-like representations there in the absence of retinal input.

We report here content-related activation during imagery in small subsets of the ventral temporal and dorsal occipital regions that responded differentially to houses, faces, and chairs during perception. Visual imagery also evoked activity in parietal and frontal cortex, but this activity was not content related. Our findings indicate that content-related activation in extrastriate cortex during imagery is implemented by “top-down” mechanisms in parietal and frontal cortex that mediate retrieval of object representations from long-term memory and their maintenance through visual imagery.

Results

Activations were measured in 9 subjects by comparing MR images obtained during performance of the following tasks: perception (passive viewing of houses, faces, and chairs); perception-control (passive viewing of scrambled pictures); imagery (generation of vivid images of familiar houses, faces, and chairs from long-term memory while viewing a gray square); and imagery-control (passive viewing of a gray square) (for details see Experimental Procedures and Figure 1). In the following sections, we present our findings of differential activations in ventral temporal and occipital cortex evoked by visual perception and visual imagery of houses, faces, and chairs. We then present our findings of activation during visual imagery in parietal and frontal cortex.

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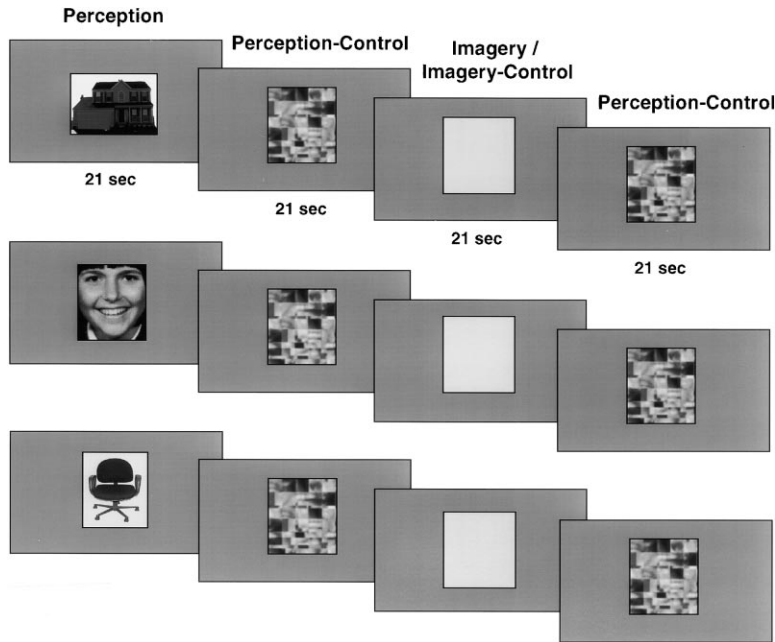


Figure 1. Stimuli and Tasks

In the perception condition, gray-scale photographs of houses, faces, and chairs were presented at a rate of 1/s for 21 s. The perception-control was scrambled pictures of these objects. In the imagery condition, a gray square was presented for 21 s, and subjects were instructed to generate vivid images of familiar houses, faces, and chairs from long-term memory. In the imagery-control condition subjects passively viewed the gray square.

Activation in Ventral Temporal Cortex

We found three bilateral regions in ventral temporal cortex that consistently showed significantly different responses during passive viewing of photographs of houses, faces, and chairs (Figure 2; Table 1). A region in the medial portion of the fusiform gyrus (MFG), including the collateral sulcus, responded maximally to houses. An adjacent region in the lateral fusiform gyrus (LFG) and occipitotemporal sulcus responded maximally to faces. Lateral to this face-selective region, a region in the inferior temporal gyrus (ITG) responded maximally to chairs. The medial-to-lateral topological arrangement of these regions was consistent across subjects. All three regions were identified in the left hemisphere of 8 of 9 subjects and in the right hemisphere of 6 of 9

subjects. When only two category-related regions were identified (N = 1 on the left, N = 3 on the right), the medial-to-lateral topological arrangement was preserved. These results thus replicate, with an independent group of 9 subjects, our original findings of category-related activations in ventral temporal cortex (Ishai et al., 1999). Although the medial-to-lateral topological arrangement was consistent across subjects, in 5 out of the 9 subjects, some chair-selective voxels were identified in the left medial fusiform gyrus. The cluster size in 3 of these subjects was smaller than 7 voxels, however, and, therefore, did not meet our a priori criteria for statistical significance. Similarly, in 3 out of the 9 subjects, some house-selective voxels were found in the left inferior temporal gyrus (one of them is shown in

Table 1. Temporal and Occipital Regions Showing Differential Responses to Houses, Faces, and Chairs

Region	Selectivity	Hemisphere	Perception		Imagery		Coordinates		
			N	Volume (cm ³) (mean ± SD)	N	Volume (cm ³) (mean ± SD)	X	Y	Z
Ventral temporal									
Medial fusiform gyri	H > F & C	Left	9/9	3.0 ± 1.4	8/9	0.8 ± 0.7	-25	-57	-15
		Right	9/9	3.8 ± 0.9	7/9	0.7 ± 0.5	25	-56	-13
Lateral fusiform gyri	F > H & C	Left	8/9	2.1 ± 1.3	6/8	0.7 ± 0.9	-37	-60	-18
		Right	9/9	2.5 ± 1.9	5/9	0.7 ± 0.2	38	-56	-18
Inferior temporal gyri	C > F & H	Left	9/9	2.2 ± 0.9	8/9	0.3 ± 0.4	-42	-66	-11
		Right	6/9	1.8 ± 0.6	4/6	0.3 ± 0.1	43	-68	-7
Dorsal occipital									
	H > F & C	Left	9/9	3.4 ± 3.1	9/9	1.2 ± 0.9	-24	-86	21
		Right	9/9	4.2 ± 2.9	8/9	0.9 ± 0.6	32	-85	19
	C > F & H	Left	7/9	1.9 ± 1.4	7/9	0.6 ± 0.5	-23	-85	22
		Right	4/9	1.5 ± 0.7	2/4	0.3 ± 0.2	23	-83	33

Voxels showing differential responses during perception demonstrated a significant overall experimental effect ($Z > 4.0$) and a significant difference among responses to houses (H), faces (F), and chairs (C) ($Z > 1.96$). Voxels showing differential imagery responses demonstrated a significantly greater response during imagery than during the imagery-control condition ($Z > 2.58$), as well as differential responses to faces, houses, and chairs during perception. Volumes were calculated before spatial normalization. Coordinates for the perception regions are in the normalized space of the Talairach and Tournoux brain atlas. N indicates number of subjects in whom each region was identified.

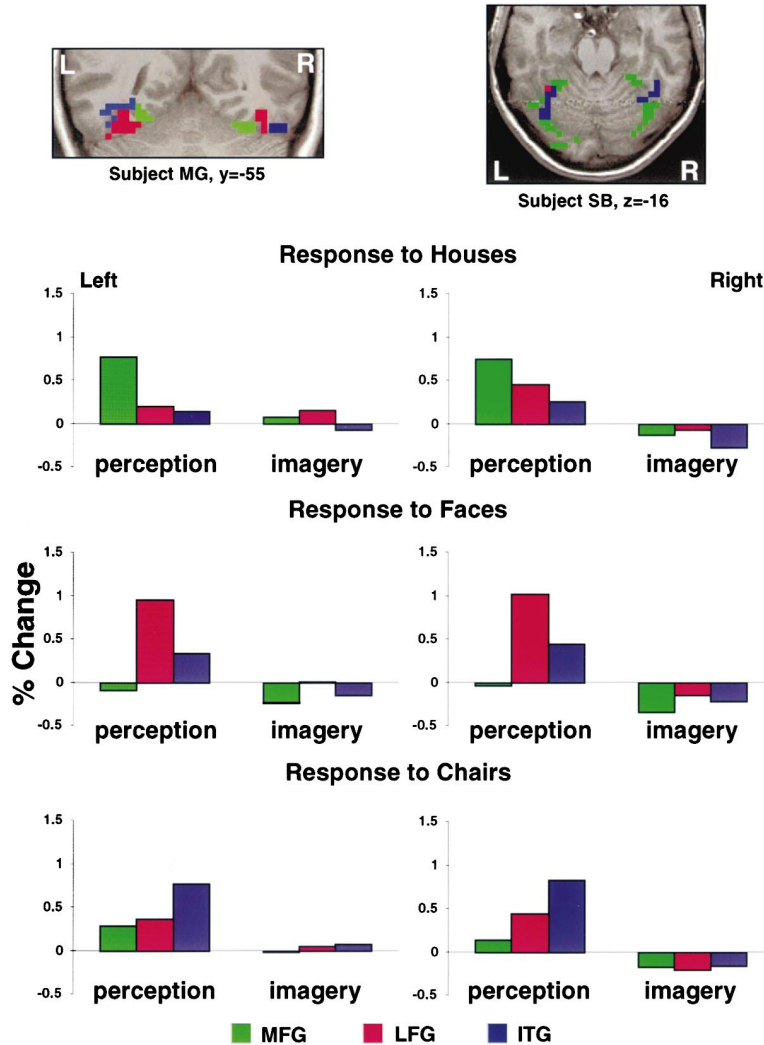


Figure 2. Response in Ventral Temporal Cortex during Visual Perception of Houses, Faces, and Chairs

Top: Locations of three ventral temporal regions that responded differentially during perception of houses, faces, and chairs, illustrated in a coronal section ($y = -55$) and an axial section ($z = -16$) from two subjects. 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 7 or more voxels). Regions showing maximal responses to houses (medial fusiform), faces (lateral fusiform), and chairs (inferior temporal) are shown in green, red, and blue, respectively.

Bottom: Mean amplitude of fMRI signal for these three ventral temporal regions. Data are averaged across all subjects and all repetitions of task blocks in each subject. Colored bars indicate response during visual perception and visual imagery of houses, faces, and chairs, within medial fusiform gyri (MFG), lateral fusiform gyri (LFG), and inferior temporal gyri (ITG).

Figures 2 and 3). The clusters were smaller than 7 voxels, and, therefore, none of these regions met our a priori criteria for statistical significance.

Averaging across the full volume of these category-related regions in ventral temporal cortex, the response during visual imagery of houses, faces, and chairs was negligible and showed no differential responses related to category (Figure 2). The comparison between the imagery and imagery-control conditions, however, showed that a subset of the voxels in these category-related regions were activated by imagery (Figures 2 and 3; Table 1). The spatial extent of cortex that was activated during imagery in these regions was only 15% of their total volume (Figure 4). Importantly, the activations during imagery in these common regions were content related. For each object category, activation during imagery was maximal in the same region that responded maximally during perception of that category (Figure 3).

To test the selectivity of the imagery response, we compared the activation evoked by imagery of each object category (e.g., houses) in the region activated maximally during perception of that category (e.g., MFG) relative to the other two regions (e.g., LFG and ITG). The results of these pairwise comparisons revealed that

imagery of houses evoked greater activation in MFG as compared with activations in the LFG and ITG ($p < 0.001$). Similarly, the activation evoked by imagery of faces was higher in LFG as compared with activations in the MFG and ITG ($p < 0.01$). Finally, the maximal activation evoked during imagery of chairs was in ITG, as compared with the activations in the MFG and LFG ($p < 0.01$).

Visual imagery evoked a stronger response in the left ventral temporal regions, while visual perception evoked a stronger response in the right (Figure 4). This effect of hemispheric asymmetry was statistically significant for the amplitude of activation ($p < 0.001$). Asymmetry of the volume of activated cortex was in the same direction but was not statistically significant ($p = 0.07$).

In the first analysis used thus far, regions with category-related responses were defined as voxels with significant differences among responses to the three object categories segregated according to which category evoked the maximal response (see Experimental Procedures). This method was used to identify the full extent of cortex that showed significant category-related responses, including voxels in which the differential response was a greater activation for two categories (e.g.,

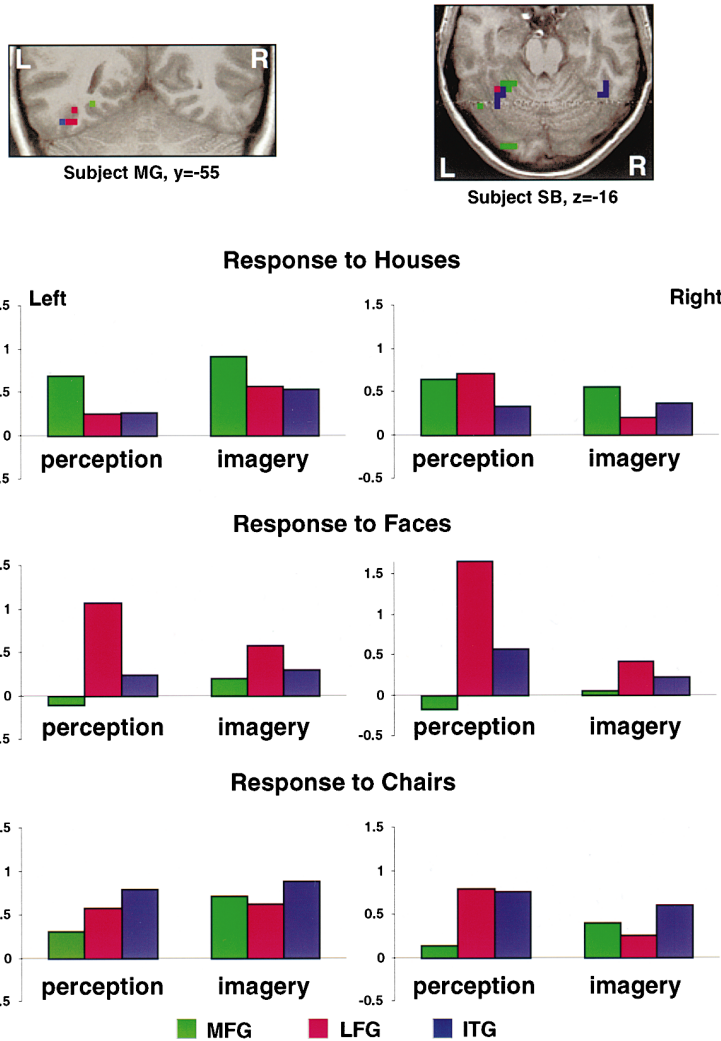


Figure 3. Response in Ventral Temporal Cortex during Visual Imagery of Houses, Faces, and Chairs

Top: Locations of three ventral temporal regions that responded differentially during imagery of houses, faces, and chairs, illustrated in a coronal section ($y = -55$) and an axial section ($z = -16$) from two subjects. Voxels shown in color demonstrated a significant response during perception, as well as an imagery response. Regions showing maximal responses during imagery of houses (medial fusiform), faces (lateral fusiform), and chairs (inferior temporal) are shown in green, red, and blue, respectively.

Bottom: Mean amplitude of fMRI signal for these three ventral temporal regions. Data are averaged across all subjects and all repetitions of task blocks in each subject. Colored bars indicate response during visual imagery and perception of houses, faces, and chairs, within medial fusiform gyri (MFG), lateral fusiform gyri (LFG), and inferior temporal gyri (ITG).

houses and chairs) as compared to the third (faces). Such voxels, therefore, demonstrate responsivity that is modulated by object category, but they are not necessarily category selective, insofar as they do not identify cortex that responds more to a single category as compared to all others tested.

Because other studies of category-related responses in ventral temporal cortex have focused on regions that respond more to a single category (Kanwisher et al.,

1997; McCarthy et al., 1997; Epstein and Kanwisher, 1998; Aguirre et al., 1998; O'Craven and Kanwisher, 2000), we performed a second analysis of our data to identify regions that demonstrated category selectivity during perception, as indicated by a significantly stronger response to one category than to the other two, allowing more direct comparison between our results and those of others. As expected, category-selective regions defined by this criterion were smaller and found in fewer

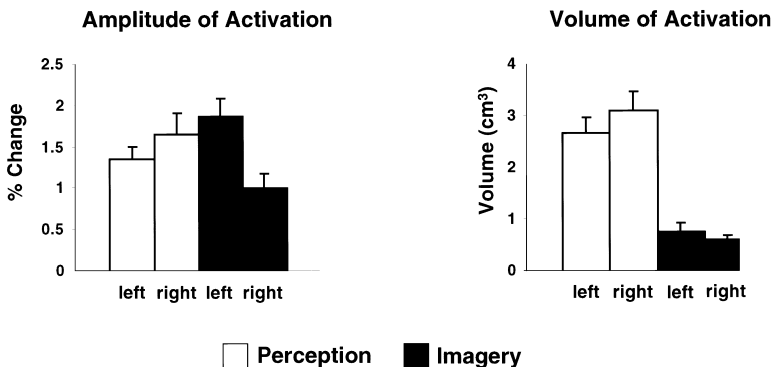


Figure 4. Amplitude (Left) and Volume (Right) of Response in Ventral Temporal Cortex during Perception and Imagery of Houses, Faces, and Chairs

The bars indicate the mean amplitude of fMRI signal and volume of cortex activated averaged across all subjects and all object categories in all regions (medial fusiform, lateral fusiform, and inferior temporal gyri). Error bars indicate standard error of the mean. Amplitudes of response are shown for the common regions activated during both perception and imagery.

Table 2. Perception

Region	First Analysis	N	Second Analysis	N	Overlap
Left MFG	52 ± 26	9	27 ± 18	8	24 (90%)
Right MFG	67 ± 26	9	38 ± 21	9	36 (93%)
Left LFG	40 ± 30	8	20 ± 17	6	19 (96%)
Right LFG	45 ± 41	9	20 ± 22	8	18 (95%)
Left ITG	36 ± 14	9	12 ± 10	6	11 (92%)
Right ITG	32 ± 12	6	8 ± 7	4	8 (97%)

Number of house-, face-, and chair-selective voxels (mean ± SD). First analysis, voxels were defined based on the omnibus test of differences among all categories. Second analysis, voxels were defined based on simple contrasts: houses versus faces and chairs; faces versus houses and chairs; chairs versus houses and faces. N indicates the number of subjects in whom each region was identified. Overlap indicates the number of category-selective voxels identified in the second analysis that were contained in the category-related regions that were identified in the first analysis.

subjects than the category-related regions identified in the first analysis (see Table 2; Figure 5). Nonetheless, these category-selective regions were comprised almost entirely of voxels that were in the larger category-

related regions, thus demonstrating the same topological arrangement as the regions identified in the first analysis.

The “common regions” in the second analysis, namely, those regions that demonstrated a general response during imagery and category-selective responses during perception (Table 3; Figure 6), were also smaller than the common regions identified in the first analysis but, nonetheless, showed a similar pattern of category-related activation during imagery. As in the first analysis, the maximal activation during visual imagery of houses was in MFG as compared with activations in the LFG and ITG ($p < 0.001$). Visual imagery of faces evoked maximal activation in LFG ($p < 0.001$). The response during visual imagery of chairs in ITG was not statistically greater than activations in the MFG and LTG, but this test was based on a much smaller number of common regions in the ITG than was found in the first analysis (5 as compared to 12).

We also tested whether opposite patterns of hemispheric asymmetry could be detected with the second, more stringent analysis. As in the first analysis, we found that visual imagery activated the left ventral temporal

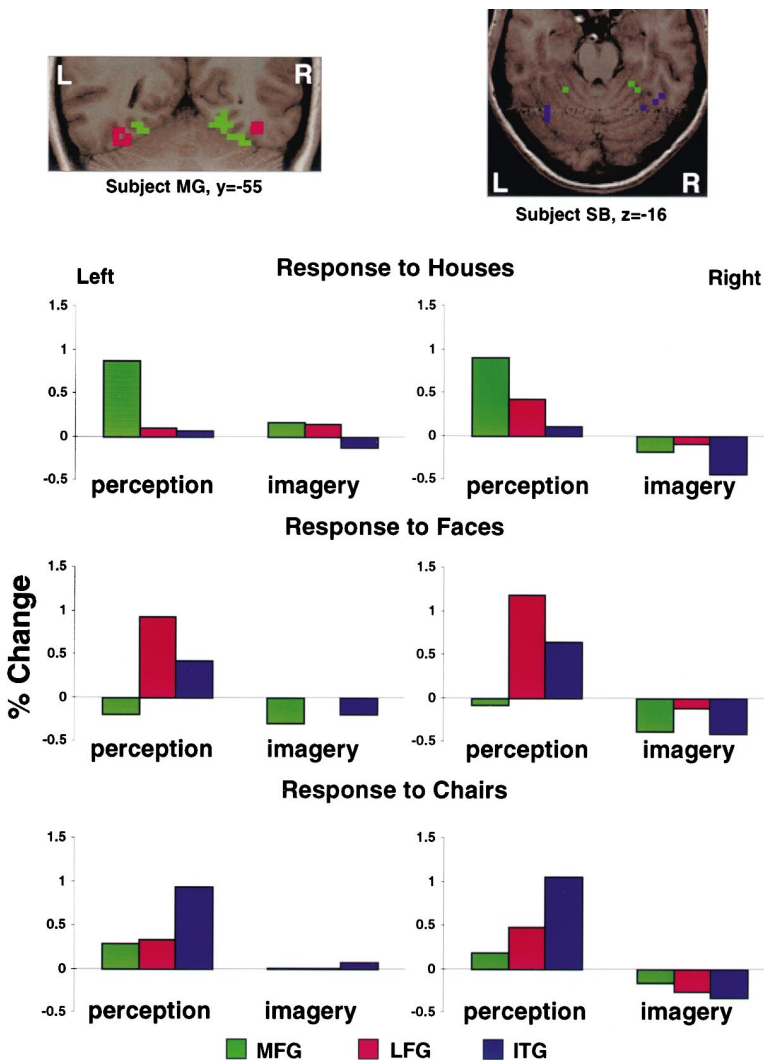


Figure 5. Response in Ventral Temporal Cortex during Visual Perception of Houses, Faces, and Chairs

Top: Locations of three ventral temporal regions that responded differentially during perception of houses, faces, and chairs, illustrated in a coronal section ($y = -55$) and an axial section ($z = -16$) from two subjects. Voxels shown in color were identified in the second analysis (see text) based on the contrasts: houses versus faces and chairs; faces versus houses and chairs; and chairs versus houses and faces. Regions showing maximal responses to houses (medial fusiform), faces (lateral fusiform), and chairs (inferior temporal) are shown in green, red, and blue, respectively.

Bottom: Mean amplitude of fMRI signal for these three ventral temporal regions (compare with Figure 2).

Table 3. Common Regions

Region	First Analysis	N	Second Analysis	N	Overlap
Left MFG	13 ± 10	7	6 ± 4	7	6 (100%)
Right MFG	11 ± 7	7	5.6 ± 3.8	7	5.3 (94%)
Left LFG	14 ± 18	6	9 ± 10	4	8.5 (94%)
Right LFG	12 ± 4	5	4 ± 2	5	3.8 (97%)
Left ITG	6 ± 6	8	4 ± 3	4	3.5 (88%)
Right ITG	5 ± 1.9	4	2 ± 0	1	2 (100%)

Regions that showed both a significant activation during imagery, as indicated by the contrast between the imagery and imagery control conditions, and a category-related (first analysis) or category-selective (second analysis) response during visual perception. N indicates the number of subjects in whom each region was identified. Overlap indicates the number of category-selective voxels identified in the second analysis that were contained in the category-related regions that were identified in the first analysis.

regions more than the right ($p < 0.01$). The asymmetry in the perception condition, however, was not statistically significant ($p = 0.3$). Note again that these statistical comparisons were performed on fewer subjects.

In sum, in the first analysis we applied a more inclusive definition of cortex, demonstrating category-related responses during perception and demonstrated category-related responses during imagery for all three object categories and greater imagery-related activations in the left as compared to the right hemisphere (Table 1; Figures 2 and 3). In the second analysis, we used a more restrictive definition of category-selective responses to facilitate comparison with the work of others. Nonetheless, we found a similar pattern of category-related responses during imagery and left-sided lateralization for imagery activations, but category-related activations during imagery were significant for only two of the three categories.

Activation in Occipital Cortex

We recently demonstrated that category-related patterns of activation are also found in ventral and dorsal occipital cortex (Ishai et al., 2000). Within ventral occipital cortex, perception of houses, faces, and chairs differentially activated the posterior fusiform (PFG), inferior occipital (IOG), and mid occipital (MOG) gyri, respectively. These regions were also identified in the present study during the perception condition (PFG, $N = 9$ subjects bilaterally; IOG, $N = 5$ and $N = 6$ on the left and right, respectively; MOG, $N = 8$ and $N = 5$ on the left and right, respectively). Only a few subjects, however, showed activation during imagery in these regions (PFG, $N = 5$ bilaterally; IOG, $N = 4$ and $N = 2$ on the left and right, respectively; MOG, $N = 4$ and $N = 0$ on the left and right, respectively). Although these results suggest that ventral occipital cortex is less involved in the representation of the content of visual images than is ventral temporal cortex, the small number of subjects who showed activation during imagery in two or more category-related regions precluded analysis of content-related patterns of response during imagery in ventral occipital cortex.

Within dorsal occipital cortex, we found regions that are category selective insofar as they respond more

during the perception of houses and chairs than during the perception of faces (Haxby et al. 1999; Ishai et al., 2000). In the present study, we confirmed those findings (Figure 7; Table 1) and again did not find any consistent pattern in the location of the clusters of voxels maximally responsive to houses relative to those maximally responsive to chairs (Figure 7; see also Ishai et al., 2000). As in ventral temporal cortex, responses in dorsal occipital cortex during visual imagery, averaged over the full volume of the regions that showed category-related perceptual responses, were negligible (as indicated by the gray bars, Figure 7A). When we analyzed only the subsets of voxels that also showed significant activation during imagery, we found that activation to be content related, as indicated by a greater response during imagery of houses and chairs than during imagery of faces (Figure 7B). Imagery of houses and chairs, however, did not evoke differential responses in these regions (Figure 7B).

We found no evidence for activation of calcarine cortex during visual imagery of houses, faces, and chairs.

Activation in Parietal and Frontal Cortex

Visual imagery, as compared with passive viewing of the gray square during the imagery-control condition, also activated several regions in parietal and frontal cortex (Figure 8). Mean brain atlas coordinates for these regions are presented in Table 4. Interestingly, the response during perception in all of these regions was negligible (Figure 8). In parietal cortex, generation of visual images activated the intraparietal sulcus and the superior parietal lobule, as well as the precuneus. In frontal cortex, visual imagery activated the caudal anterior cingulate cortex, the superior frontal sulcus, and the inferior, mid and superior frontal gyri. Visual imagery also evoked activation in the cerebellum (Table 4).

In all these parietal and frontal regions of interest, the response during perception and imagery was not content related. For example, in caudal anterior cingulate, responses during visual perception of houses, faces, and chairs were 0.1% for all categories, and responses during visual imagery of houses, faces, and chairs were 0.4%, 0.6%, and 0.5%, respectively. It is worth noting that the analysis of these regions was based on the contrast between imagery and imagery-control. As we did not find consistent patterns of category-related clusters during perception in parietal and frontal cortex, we could not apply the common region analysis (i.e., selection of voxels that demonstrated both category-related response during perception and an imagery response).

Discussion

In the present study, we investigated the organization of human neural systems that participate in the generation of visual images of objects stored in long-term memory. We examined whether imagery evokes patterns of response in the visual cortex that are content related. We found, using fMRI, that the perception of houses, faces, and chairs consistently evoked differential patterns of activation in ventral temporal and dorsal occipital cortex. Imagery also evoked content-related patterns

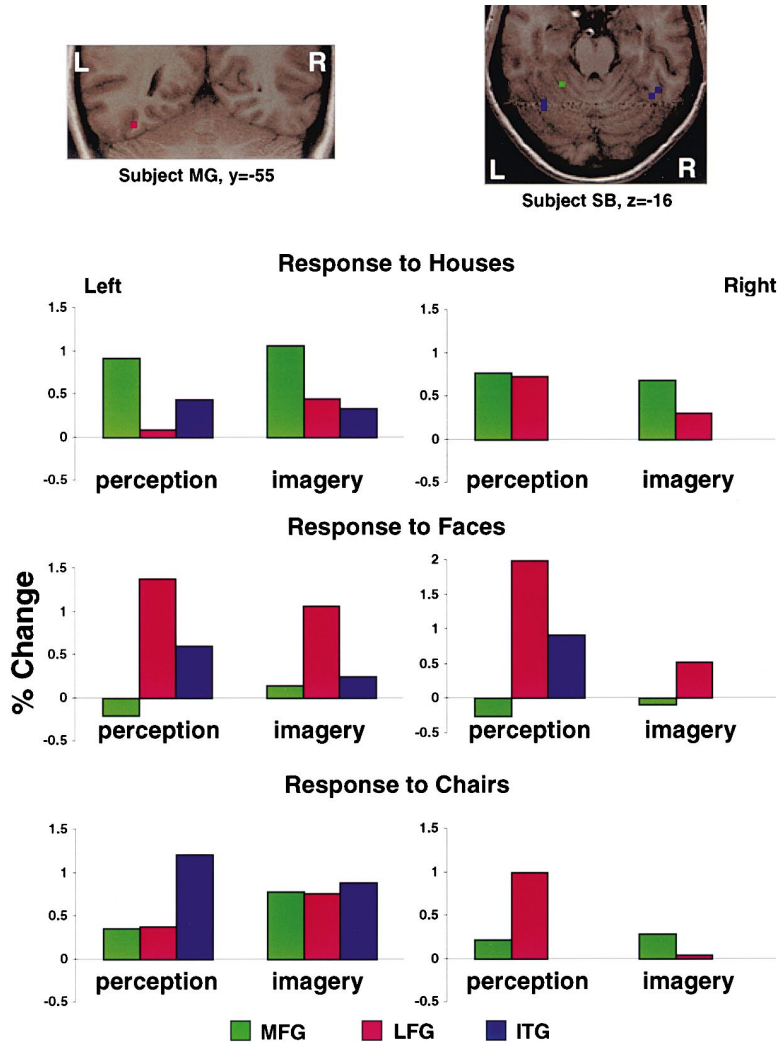


Figure 6. Response in Ventral Temporal Cortex during Visual Imagery of Houses, Faces, and Chairs

Top: Locations of three ventral temporal regions that responded differentially during imagery of houses, faces, and chairs, illustrated in a coronal section ($y = -55$) and an axial section ($z = -16$) from two subjects. Voxels shown in color were identified in the second analysis (see text) based on the contrasts: houses versus faces and chairs; faces versus houses and chairs; and chairs versus houses and faces.

Bottom: Mean amplitude of fMRI signal for these three ventral temporal regions (compare with Figure 3).

of activation in these regions, but this activity was restricted to small sectors of the regions that responded differentially during perception. Visual imagery and visual perception evoked activity with opposite patterns of hemispheric asymmetry in ventral temporal cortex, with imagery evoking stronger responses on the left and perception evoking stronger responses on the right. We also found activation during imagery, but not during perception, in regions of parietal and frontal cortex, which may mediate the “top-down” control of generating and maintaining mental images.

The perception of houses, faces, and chairs evoked maximal activation in medial fusiform, lateral fusiform, and inferior temporal gyri, respectively, with a consistent medial-to-lateral topological arrangement. Moreover, houses and chairs evoked more activation in regions of dorsal occipital cortex than did faces. These findings replicate our previous reports (Ishai et al., 1999, 2000). We identified the category-related perceptual responses in order to compare them with responses evoked by imagery. Our results demonstrated that the response during imagery, when averaged across the full volume of cortex activated during perception, was negligible. However, when we looked at only the subsets

of the category-related regions that also showed activation during imagery, we found content-related patterns of response during imagery. In ventral temporal cortex, for each category, activation during imagery was maximal in the same region that responded maximally during perception (e.g., imagery of faces evoked maximal activation in the lateral fusiform “face-selective” region). It is of interest that the category-related activation during both perception and imagery was independent of the statistical criteria by which the voxels were selected. The more stringent criteria identified smaller regions in fewer subjects. The differential activation evoked by houses, faces, and chairs in these smaller regions, however, was virtually identical to the activation found in the larger regions identified using a more inclusive definition of cortex demonstrating category-related responses.

Additional evidence for content-related activation during imagery in ventral temporal cortex has been recently reported by O’Craven and Kanwisher (2000), who found that the regions involved during perception of faces and scenes were also recruited during visual imagery. We also found that imagery of houses and chairs evoked more activation as compared to imagery of faces

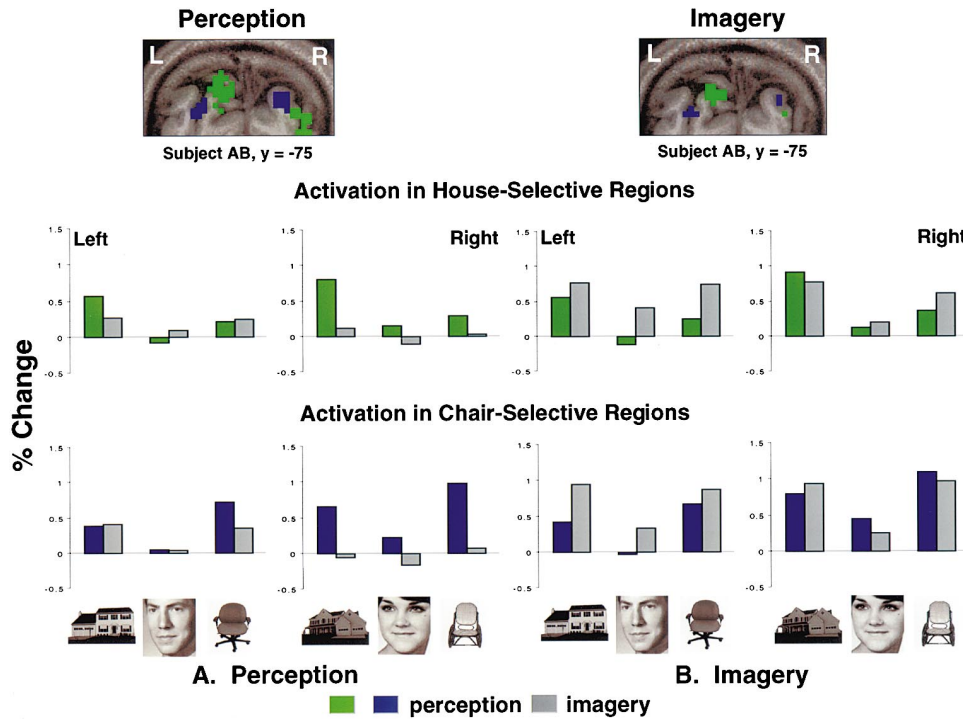


Figure 7. Response in Dorsal Occipital Cortex during Visual Perception (A) and Visual Imagery (B) of Houses, Faces, and Chairs

Top: Clusters that responded differentially to houses (green) and chairs (blue), illustrated in a coronal section ($y = -75$) from a single subject. In the perception condition, voxels shown in color demonstrated a significant overall experimental effect ($Z > 4.0$) and a significant difference among responses to houses and chairs ($Z > 1.96$, clusters of 7 or more voxels). In the imagery condition, voxels shown in color demonstrated a significant category-related response, as well as an imagery response.

Bottom: Mean amplitude of fMRI signal. Data are averaged across all subjects and all repetitions of task blocks in each subject. Colored bars indicate response during visual perception of houses, faces, and chairs. Gray bars indicate response during visual imagery of these object categories.

in dorsal occipital cortex. These results suggest that small sectors of extrastriate regions that participate in visual perception of objects are also involved in representing perceptual information retrieved from long-term memory during visual imagery of these objects.

Our results suggest that sensory representations of objects stored in ventral temporal cortex are reactivated during the generation of visual images. Interestingly, electric stimulation of regions in the temporal lobe of humans results in imagery recall, suggesting that memory traces are localized in these regions (Penfield and Perot, 1963). Neuropsychological case studies have also implicated the temporal lobe as the location of the storehouse for visual memories. For example, perception and imagery are both impaired in patients with face and object agnosia due to occipitotemporal lesions (Levine et al., 1985). Moreover, patients with semantic dementia, due to atrophy of the anterior-inferior temporal lobe, perform poorly on tests that require knowledge about people and objects, such as picture naming and drawing objects from memory (for a review see Graham et al., 1999). Finally, studies in nonhuman primates indicate that the temporal lobe is the memory storehouse for visual representations of complex stimuli (Miyashita and Chang, 1988; Miyashita, 1988). Taken together, these findings indicate that visual representations stored in ventral temporal regions are reactivated during memory retrieval and visual imagery.

It is unclear why imagery evokes activity in only a small portion of the visual extrastriate regions that participate in perception. It is possible that the representation of perceptual information that is evoked by imagery is simply weaker than equivalent representations evoked by retinal input. Alternatively, only a specific subset of extrastriate cortex may be dedicated to mental imagery, allowing perception and imagery to operate simultaneously.

Visual imagery and visual perception evoked activity with opposite patterns of hemispheric asymmetry in ventral temporal cortex. Visual imagery evoked stronger responses on the left, whereas visual perception evoked stronger responses on the right. Other physiological and functional brain imaging studies have reported that image generation is asymmetrically localized to the left hemisphere. For example, Farah and colleagues have found that the event-related potentials associated with the generation of mental images were greater on the left posterior temporal site than on the right (Farah et al., 1989). More recently, D'Esposito and colleagues have found, using fMRI, that when subjects generated mental images of the referents of concrete nouns, the left inferior temporal lobe (Brodmann's area 37) was "the most reliably and robustly area activated" (D'Esposito et al., 1997). The large left inferior temporal region that was activated more by concrete than abstract nouns appears to encompass all of the category-selective sub-

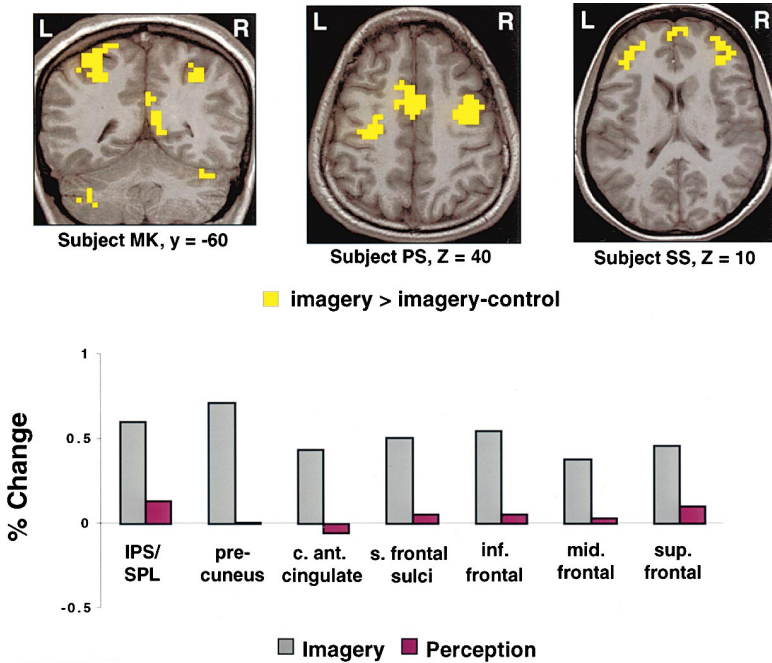


Figure 8. Regions Showing Imagery Response, as Compared with the Imagery-Control Condition

Top: A coronal section (left) showing activations in the intraparietal sulcus (IPS) and the superior parietal lobule (SPL), precuneus, and cerebellum; an axial section (middle) showing activations in caudal anterior cingulate cortex and superior frontal sulcus; an axial section (right) showing activations in mid and superior frontal gyri. Voxels shown in yellow demonstrated a significant experimental effect ($Z > 4.0$), and a significant difference between imagery and imagery-control condition ($Z > 2.58$, clusters of 7 or more voxels).

Bottom: Mean amplitude of fMRI signal during imagery and perception averaged across all subjects and all object categories in several regions of parietal and frontal cortex.

sectors that we have identified. Because D'Esposito et al. (1997) performed a group analysis only, it is unclear whether the imagery-related activations in individual subjects had more restricted spatial extents similar to what we and others (O'Craven and Kanwisher, 2000) have found. A special role for the left hemisphere in visual imagery is also supported by numerous case studies of patients with image generation impairment due to damage in left temporo-occipital areas (for a review see Farah, 1995). Other studies, however, have concluded that both cerebral hemispheres contribute equally to the generation of mental images (Sergent, 1989) or that both hemispheres can generate mental images, but in different ways (Kosslyn et al., 1995b).

Our findings demonstrated that both hemispheres were activated by our imagery task, albeit asymmetrically. Hypotheses about different roles for the left and right hemispheres in generating visual images can be tested directly by manipulating the mental images subjects generate.

We found no evidence for calcarine activation during visual imagery of houses, faces, and chairs. Our findings agree with some previous reports (Roland and Gulyas, 1994; Mellet et al., 1996, 1998; D'Esposito et al., 1997), but not others that did find activation in early visual areas during imagery (Le Bihan et al., 1993; Kosslyn et al., 1993, 1995a, 1999; Chen et al., 1998). As different researchers have used tasks that required different

Table 4. The Cerebellum, Parietal, and Frontal Regions Showing Responses during Imagery, Relative to the Imagery-Control Condition

Region	Hemisphere	N	Volume (cm ³) (mean ± SD)	Coordinates		
				X	Y	Z
Cerebellum	Left	4/4	1.8 ± 1.4	-31	-58	-31
	Right	3/4	2.3 ± 2.6	31	-62	-36
Precuneus	Left	6/9	1.9 ± 1.5	-10	-61	27
	Right	6/9	1.1 ± 1.0	7	-71	32
Intraparietal sulci/superior parietal	Left	9/9	3.2 ± 1.5	-29	-60	40
	Right	6/9	3.2 ± 1.4	32	-55	48
Caudal anterior cingulate	Left	5/5	2.2 ± 1.1	-6	10	33
	Right	5/5	1.7 ± 0.5	9	11	32
Superior frontal sulci	Left	5/5	2.9 ± 1.2	-30	2	41
	Right	3/5	2.5 ± 1.9	34	2	40
Inferior frontal gyri	Left	4/5	3.6 ± 3.2	-39	20	12
	Right	3/5	3.8 ± 0.7	40	14	10
Mid frontal gyri	Left	4/5	3.8 ± 2.4	-28	44	11
	Right	4/5	3.9 ± 1.9	35	38	10
Superior frontal gyri	Left	4/5	2.7 ± 0.9	-10	54	11
	Right	4/5	3.4 ± 0.9	17	52	8

Volumes were calculated before spatial normalization. Coordinates are in the normalized space of the Talairach and Tournoux brain atlas. N indicates number of subjects in whom each region was identified. Frontal regions were scanned in only the 5 subjects with axial scans. The cerebellar regions were consistently visible in only the 4 subjects with coronal scans.

types of memory (short versus long term) and/or had different baseline conditions, it is difficult to account for the conflicting findings. In our paradigm, subjects were instructed to generate vivid images from long-term memory but were not asked to manipulate or scrutinize the images. It is possible that in order to evoke activation in early visual areas, subjects need to focus their attention on features of the mental images they form. Sakai and Miyashita (1994) suggested focal attention as the mechanism by which the primary visual cortex is recruited during imagery. According to their model, 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.

Visual imagery, as compared with the imagery-control condition, also activated several parietal and frontal regions that have been implicated in "top-down" control functions, but the activity in these regions was not content related. The perceptual response to photographs of houses, faces, and chairs within these parietal and frontal regions was negligible. In the parietal lobe, visual imagery evoked activation in the intraparietal sulcus and the superior parietal lobule, regions involved in a variety of spatial and nonspatial 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). In the frontal lobe, visual imagery activated the caudal anterior cingulate cortex, the superior frontal sulcus, and the inferior, mid, and superior frontal gyri. All of these frontal regions are involved in visual working memory (Courtney et al., 1997; 1998; Petit et al., 1998; Haxby et al., 2000a). Our findings suggest that the generation of visual images of objects involves both the category-related regions of extrastriate cortex and a network of parietal and frontal regions. These parietal and frontal regions may mediate the retrieval of object representations from long-term memory, their maintenance in a working memory "buffer," and the attention required to generate those mental images. Mental imagery of objects appears to be, thus, 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 results were reported in a study of motion imagery (Goebel et al., 1998), which found activation in a network composed of motion-sensitive regions MT/MST and prefrontal areas (FEF and BA 9/46).

In sum, our findings propose a new perspective on the neural basis of visual imagery. Mental imagery of objects shares common neural substrates with visual perception only to the extent that small sectors of the category-related perceptual regions also show content-related activation during imagery. Neural activity evoked in these regions may reflect the representation of the visual content of images. Moreover, several parietal and frontal regions that do not respond during perception participate in the generation of visual images. This parietal and frontal network mediates the "top-down" control of retrieving pictorial information from long-term memory and holding mental images in the "mind's eye."

Experimental Procedures

Subjects

Nine normal, right-handed subjects (4 males, 5 females, age 28 ± 5 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 and Tasks

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. In the perception condition, gray scale photographs of houses, faces, and chairs were presented at a rate of 1/s for 21 s in a classic block design, and subjects were instructed to view the stimuli. During the perception-control condition, subjects passively viewed scrambled pictures. In the imagery condition, subjects were instructed to generate images of familiar houses, faces, or chairs from long-term memory while viewing a gray square. During the imagery-control condition, subjects passively viewed the gray square (Figure 1). In 6 runs, the perception condition was followed by the imagery condition. In the other 6 runs, the perception condition was followed by the imagery-control condition. Imagery and imagery-control runs alternated. The order of category blocks was counterbalanced across runs. Imagery of one object category was preceded by perception of that category (e.g., after passively viewing chairs, subjects were cued to generate vivid mental images of familiar chairs from long-term memory). Before the scanning session, subjects were pretrained with the imagery task. During postscan debriefing, all subjects reported generating clear and reasonably vivid images of familiar houses, faces, and chairs.

Data Acquisition

A 1.5T General Electric Signa scanner with whole head RFD coil was used. Changes in blood oxygen level-dependent T2*-weighted MRI signal were measured using a gradient-echo echoplanar sequence (TR = 3 s, TE = 40 ms, FOV = 20 cm, 64×64 matrix, voxel size = $3.125 \times 3.125 \times 5$ mm). In each time series, 91 volumes, each containing 18, 5 mm thick coronal slices (N = 4 subjects) or 24, 5 mm thick axial slices (N = 5 subjects) 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 or axial slices, TR = 13.9, TE = 5.3, 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 et al., 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 s and with a standard deviation equal to the estimated temporal dispersion of 1.8 s (Maisog et al., 1995). Temporal autocorrelations in the fMRI time series were corrected using an algorithm based upon the variance of derivatives approach (Worsley and Friston, 1995). The corrected number of error degrees was $\sim 70\%$ of the total degrees of freedom on the entire time series. All statistical tests were adjusted so that they were based on this reduction in the number of independent observations because of temporal autocorrelations.

The responses to the different object categories were analyzed using multiple regression (Friston et al., 1995; Haxby et al., 2000b). The multiple regression model included the following 9 orthogonal contrasts: all tasks versus baseline; perception versus imagery and imagery-control; imagery versus imagery-control; faces versus houses and chairs; houses versus chairs; imagery faces versus im-

imagery houses and imagery chairs; imagery houses versus imagery chairs; imagery-control faces versus imagery-control houses and imagery-control chairs; imagery-control houses versus imagery-control chairs. The contrasts: faces versus houses and chairs, and houses versus chairs were designed to identify the brain regions that responded differentially during perception (see also Ishai et al., 1999, 2000). Similarly, the contrasts imagery faces versus imagery houses and imagery chairs, and imagery houses versus imagery chairs were designed to identify regions showing content-related activation during imagery. Waveforms representing these 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 mean intensity and 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.

The statistical significance of the clusters of voxels was assessed based on their spatial extent (Friston et al., 1994). We identified voxels that demonstrated significant category-related responses during perception using two sets of criteria. For both sets of criteria, voxels were selected that showed a significant experimental effect ($Z > 4.0$) for the combined effect of the three regressors of interest in the analysis of all 12 time series and an overall increase in activity for meaningful stimuli (a positive regression weight for the contrast between meaningful and control stimuli). In our first analysis, voxels with category-related responses were defined as those that showed a significant differential category effect based on an omnibus test of response differences among categories ($Z > 1.96$, $p < 0.025$, for the combined effect of the second and third regressors). Voxels were then segregated into clusters of 7 or more contiguous voxels according to the category of objects that evoked the maximal response (a cluster of this size had a statistical significance of $p < 0.05$ in each subject). These criteria identify all voxels that show any differences in responses to different categories. We performed a second analysis of ventral temporal cortex using a more restrictive definition of category-selective responses in which voxels were identified that showed a significantly greater response for one category (e.g., houses) than the other two (e.g., faces and chairs) based on a simple contrast ($Z > 1.96$, $p < 0.05$). This criterion therefore excludes voxels in regions that may have significant category-related responses but are not category-selective. For example, it would exclude voxels showing a strong response evoked by two categories (e.g., houses and chairs) and a weak response evoked by the other category (e.g., faces). We include the results of this analysis to facilitate comparison between our results and those of others who use the more restrictive definition of category-selective responses. In the regional analysis of the imagery condition, voxels were selected that showed a significant experimental effect ($Z > 4.0$) and a significantly greater response during imagery than during the imagery-control condition ($Z > 2.58$, $p < 0.005$, clusters of 7 or more voxels).

The results of the differential imagery effects showed that content-related imagery activation, defined by statistical significance within individual voxels, was found in only a few subjects (activation in medial fusiform was identified bilaterally in 6 subjects, in lateral fusiform in 3 subjects on the right and none on the left, and in inferior temporal in 2 subjects on the right and 4 on the left). In order to examine content-related activation in a larger portion of our subjects, we therefore selected voxels that showed both category-related responses (first analysis) or category-selective responses (second analysis) during perception, and general activation during imagery (imagery versus imagery-control). The criteria for selecting these voxels, therefore, did not bias the subsequent statistical tests for the significance of content-related imagery responses. These common regions were found in more subjects (see Tables 1 and 3), and the spatial extents of the activation were larger than those identified by the statistical significance of content-related imagery effects in individual voxels.

For each subject and each region, a mean time series averaged across voxels in the region and across repetitions of blocks with the same condition was calculated. 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 task baseline (scrambled pictures in the perception condition; gray square in the imagery condition). The significance of content-related patterns of activation during imagery was tested for each category using pairwise t tests to examine the difference between activation in the region that responded maximally to that category during perception (e.g., the MFG for houses) and activation in the regions that responded maximally to the other categories during perception (e.g., the LFG and ITG).

The anatomical locations of clusters of voxels showing significant differences during perception and imagery 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 et al., 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 during perception and imagery of houses, faces, and chairs.

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