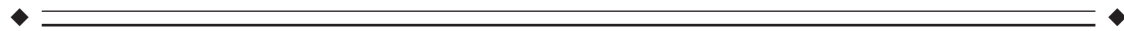# Neural Correlates of Visual Form and Visual Spatial Processing

Liming Shen,* **Xiaoping Hu, Essa Yacoub, and Kamil Ugurbil**

*Center for Magnetic Resonance Research, Department of Radiology,
University of Minnesota, Minneapolis, Minnesota*

Abstract: Cortico-cortical projections for visual processing that originate from the striate cortex are organized into two streams. The dorsal stream projects to the parietal region and the ventral stream to the inferior temporal region. One hypothesis is that the dorsal stream processes visual spatial information, and the ventral stream processes visual object information. Although recognition of human faces or common objects has been shown preferentially to activate the ventral stream, the issue of when such processing starts to engage the ventral or the dorsal stream is not clear. The question explored in this study is whether processing of visual form per se without evoking the brain mechanisms that are associated with recognition of human faces or common objects is sufficient to activate the ventral stream more significantly relative to the condition when only visual spatial processing is involved. Functional magnetic resonance images were acquired while subjects performed a delayed comparison task in which either visual spatial or visual form information was processed. Cortical areas that were preferentially activated in visual spatial or visual form processing showed not only ventral-dorsal segregation, but also hemispheric laterality. The results extended previous findings by showing that preferential activation in the ventral pathway is not contingent upon such powerful stimuli as faces and common objects. Processing of simple visual form information is cause enough for such activation to be observed. A strong left hemisphere dominance in visual form recognition was also revealed. The observed laterality may be a reflection that the left hemisphere is more important in symbolic and/or semantic coding of visual form information. *Hum. Brain Mapping 8:60–71, 1999.* © 1999 Wiley-Liss, Inc.

Key words: object recognition; hemispheric laterality; working memory; functional imaging
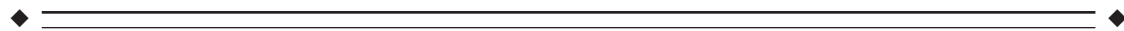
INTRODUCTION

It has been proposed that the cortico-cortical projections for visual processing that originate from the striate cortex are organized into two functionally and anatomically separate pathways, a dorsal stream that reaches the posterior parietal cortex and a ventral stream that goes to the inferior temporal region [Ungerleider and Mishkin, 1982]. The two streams then project to the frontal cortex via different pathways [Boussaoud et al., 1995]. One theory is that object recognition occurs in the ventral pathway, whereas spatial localization occurs in the dorsal pathway, the so-called where and what hypothesis [Ungerleider and Mishkin, 1982]. Another is that visual processing for perception occurs in the ventral pathway, whereas visual processing for action occurs in the dorsal pathway, the so-called perception and action hypothesis [Goodale and Milner, 1992]. The current study ex-

plored the issue by mapping brain regions activated with fMRI while human subjects engaged in a perceptual task in which they either focused their attention on the spatial location of a visual stimulus or on its visual pattern, without making concurrent motor responses.

There have been a number of studies that explicitly contrasted brain regions for object recognition vs. spatial processing [Clark et al., 1996; Courtney et al., 1996; Haxby et al., 1991; Haxby et al., 1994; Kohler et al., 1995]. The stimuli employed in these studies were either pictures of human faces or line drawings of common objects. Since these stimuli all have strong semantic meanings, object recognition in these studies included both the recognition of visual forms [Ullman, 1989] and the association of the perceived visual forms with related semantic or episodic memories [Farah, 1990]. Consequently, the observed activation includes not only structures for visual processing, but also memory processes that are associated with face or object recognition. Of interest here is whether visual form recognition per se suffices to elicit the differential activation in the ventral and the dorsal pathways generally observed in these studies. Contrasting visual form recognition vs. spatial recognition is also conceptually more balanced than contrasting face or object recognition vs. spatial recognition in the sense that visual form recognition should not evoke memories that assign meanings to a face or a common object, but not to a spatial location. Another issue with previous studies is that they all involve concurrent motor output, possibly confounding the perceptual tasks with an action component, which is expected to activate multiple regions in the parietal and frontal cortex [Grafton et al., 1996; Sakai et al., 1998]. Additionally, complex stimuli such as faces elicit complex patterns of eye movements [Yarbus, 1967], and such eye movements could conceivably be different when a subject's attention is directed toward recognizing a particular face and when it is employed in determining the location of it in space. The present study explores the differential processing of "what" vs. "where" information, with a paradigm that addresses these issues.

METHODS

Subjects

Nine healthy, right-handed volunteers, as tested by the Edinberg Handedness Tests [Oldfield, 1971], (6 male, 3 female, ages 20–40) gave informed consent before participating in this study. The study protocol was approved by the Institutional Review Board of the University of Minnesota.

Tasks

Blood oxygenation level dependent (BOLD)-based functional magnetic resonance imaging (fMRI) scans were carried out while subjects performed visual form recognition and spatial recognition tasks. Visual presentation for the tasks and recording of subjects' responses were controlled by a Macintosh PowerBook 180c (Cappuchino, CA) running PsyScope (http://psyscope.psy.cmu.edu/PsyScope/). The stimuli were displayed on a back-projection screen at the end of the scanner table ~10 feet from the subject's eyes. The screen subtended about a 10° visual angle and each stimulus pattern subtended a 1.4° visual angle. The subject controlled a four button keypad, which was interfaced with the Macintosh computer.

For both tasks, abstract visual patterns were presented one at a time in a random order during task periods (0.5 sec duration, 1.5 sec intertrial interval) (Fig. 1). Four possible locations on the screen and four different patterns were utilized, yielding a total of 16 location-pattern combinations. A typical scan lasted ~396 (132 images at 3 sec each) sec and was partitioned into four alternating task periods and five resting periods (Fig. 1). Each task period was 48 sec long, allowing each location-pattern combination to be presented twice. For spatial recognition, subjects watched the presentation of the stimuli and decided whether any two consecutive presentations occurred at the same spatial location and counted the total number of repetitions in the task period while ignoring the patterns of the stimuli. At the end of each task period, they pressed a button on the keypad to indicate the total number of repetitions they counted. The number of repetitions varied for each task period, typically ranging from 0–3. The keypad has four buttons arranged in a row, representing the numbers 0–3 in order. In those rare instances when the total number of repetitions was >3, subjects were instructed to press the 3 key. No three consecutive stimuli were ever presented at the same spatial location. The total number of repetitions was designed to impose a minimum mental load. This deferred response mode ensured that the subject's performance was monitored while avoiding overt motor responses during the task period. For visual recognition, subjects watched the same visual display and decided if any two consecutive displays were of the same visual pattern. Again, they counted the total number of repetitions and pressed a button to indicate their results after the task period ended. During the resting period, subjects focused on a crosshair displayed at the center of the screen. The order of the spatial and visual recognition blocks was counterbalanced across subjects.
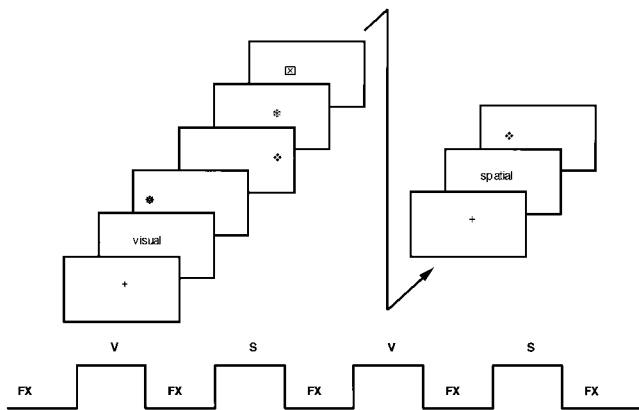
Experimental Paradigm

Figure 1.

Experimental paradigm employed in this study. Upper portion shows consecutive presentation; bottom portion shows overall time line of presentation. Four task periods are interleaved with periods of simple visual fixation. A one word instruction was given before each task period, followed by presentation of the visual stimulus. FX = period of visual fixation in which a center crosshair was presented; V = period of visual form recognition task; S = period of spatial recognition task.

FMRI studies

The study was carried out on a 1.5 T Siemens Vision system (Siemens Medical Systems, Iselin, NJ). Functional images were acquired with a T2*-weighted echo planer imaging (EPI) sequence (TE = 60 msec; TR = 3000 msec; field of view = 24 cm × 24 cm; matrix = 64 × 64; number of slice = 20; thickness = 5 mm; gap = 1 mm). Oblique axial slices were prescribed to cover the entire brain with a minimum number of slices and to avoid artifacts caused by eye movements [Chen and Zhu, 1997]. T1-weighted anatomical images were acquired with the same field of view and orientation, on a slightly thicker slab using a 3D MPRAGE (Siemens) sequence (matrix = 256 × 256; slab thickness = 132 mm; equivalent slices = 44). Two identical functional scans were carried out on each subject.

Data analysis

Data were analyzed using Stimulate [Strupp, 1996] and various routines written in PV-wave. Each fMRI data set was first screened for subject movement by calculating the trajectory of the center-of-mass, its mean, and its standard deviation. Data with excessive head movement in both runs were discarded, and these subjects were not included in the total count.

Each data set was then corrected for misalignment from subject motion. One volume out of the 132 volumes from each scan (usually the 60th scan) was chosen as the template and other volumes were aligned to the template using a rigid body model (Automated Image Registration) [Woods et al., 1998]. Two comparisons were subsequently carried out. The first comparison was used to identify brain structures *commonly* activated in both the spatial and visual form recognition tasks. The second comparison was used to identify brain structures *differentially* activated in the two task conditions. Pixels that were commonly activated in both tasks were identified using an unpaired pixel-by-pixel t-test ($P < 0.05$), comparing pixel values in both task periods vs. in the resting periods. Pixels that were differentially activated in the visual recognition vs. spatial recognition tasks were detected by contrasting pixel values during the corresponding task periods. Two partially overlapping unpaired t-tests were performed (task periods 1 and 3 [identical tasks] vs. task period 2, $P < 0.05$, and task period 3 vs. task periods 2 and 4 [identical tasks], $P < 0.05$), and only pixels that passed both t-tests were deemed significant. This strategy effectively identified pixels that had significantly different activation in the two tasks while eliminating pixels that were merely drifting monotonically during the scan, as determined by the time courses of the activated pixels. The first five image volumes in a scan were excluded from the comparison to avoid transient signal changes before a steady state was reached. The first two volumes of each task or rest period were also excluded to eliminate transient response. To guard against false positives, activated pixels with less than two neighboring pixels activated in a plane were eliminated. This procedure increased the effective probability of false positive to $P \sim 0.005$ [Forman et al., 1995]. Individual activation maps were then transformed into Talairach coordinates [Talairach and Tournoux, 1988] using measurements from the individual's anatomical image. The transformed activation maps were then re-sliced as axial images, thresholded, and superimposed onto the individual's corresponding anatomical images. Activation maps from all subjects were then combined to generate the group response and superimposed onto a typical individual's transformed anatomical image for presentation. Pixels were included in the activation maps if they were activated in more than five out of nine subjects.

The observed activation in the visual recognition vs. spatial recognition task was further tested explicitly for hemispheric laterality in the third test. Maps of pixel t value computed from the second comparison above were transformed into the Talairach coordi-

nates. The *t* map for each subject was then separated into two maps containing pixels with positive or negative *t* values, respectively. One map thus contained pixels that were relatively more active in the spatial recognition condition; the other contained pixels that were more active in the visual recognition condition. A region of interest (ROI) consisted of a selected subset of the slices from each map was tested for hemispheric laterality. Each ROI was multiplied with a mask, such that pixels in the left side of the brain were assigned positive value and the right side negative value. The average *t* value of all pixels with confidence level >0.5 within the ROI and the corresponding variance were then calculated. This average was taken as a laterality index. A significantly >0 value of the index indicates left hemispheric dominance, and vice versa.

Several considerations went into the selection of the index. One was that the threshold for voxel inclusion should be sufficiently different from that used in the second test to ensure that results from this test would not merely duplicate those from the second test simply because of the confidence level selected. Second, the inclusion of all pixels in the slices selected, rather than selecting subregions from it according to the results of the group response from the second test and then comparing their activation with symmetric regions in the opposite hemisphere, avoided problems related to hemispheric asymmetry in the locations of specific cortical areas. By making it less contingent upon the second test, the third test is less dictated by the results from the second test merely as a consequence of a thresholding artifact.

RESULTS

Behavioral data

Subjects had no difficulty performing the tasks. Of the nine data sets included in this analysis, seven were 100% correct and two contained one error out of the four responses in a run.

Neuroimaging

Areas demonstrating significant activation in both task conditions, relative to the baseline visual fixation, are listed in Table I and shown in Figure 2.

Activation common to both task conditions was consistent across subjects. In the occipitotemporal region, this included the primary visual cortex in the calcarine sulcus (Brodman's area [BA] 17), extrastriate cortex covering the middle and inferior occipital gyrus (BA 18, 19), the lateral gyrus (BA 18), and the fusiform

gyrus (BA 19). The activation extended ventrally into the inferior temporal region to the junction of BA 37 and 20, rostrally to the junction of BA 37/21 in the middle temporal gyrus, and dorsally to the posterior bank of the superior temporal sulcus in the angular gyrus (BA 39). Strong activation in the right hemisphere was seen in the superior temporal gyrus (BA 22) in the vicinity of the parietotemporal junction and extended into BA 40 of the inferior parietal cortex. Extensive bilateral activation along the intraparietal sulcus was observed in the parietal cortex, with the activation in the right hemisphere slightly more consistent and extending farther both rostrally and caudally. The activation spanned the entire rostral extent of the intraparietal sulcus and caudally into the occipital cortex.

Activation common to both tasks was also observed in the frontal cortex. In the medial wall, activation extended from the posterior superior frontal gyrus (SFG) at the approximate rostrocaudal level of the anterior commissure (CA), medial area 6, to the cingulate gyrus ~2 cm anterior to CA (BA 32, 24). The activation was more robust on the left side. On the lateral surface, bilateral activation was present in the posterior portion of SFG and laterally in the medial frontal gyrus (BA 6) and the posterior end of BA 8. The activation extended rostrally along the inferior frontal sulcus ~4 cm anterior to CA to include portions of BA 9, 44, 45, and 46 on both the medial and the inferior frontal gyrus. Additional activation was also seen bilaterally in the anterior portion of the insula and in the lateral and medial cerebellum.

Differential activation in the two tasks was observed when activation from the two task conditions was contrasted. Compared to the activation common to both tasks, the differential activation was smaller in size (Fig. 3, Table II). Additionally, strong hemispheric asymmetry was observed. Visual recognition preferentially activated the left hemisphere, whereas loci more active in the spatial recognition task lie mostly in the right hemisphere.

In the posterior cortex, the left lateral occipital cortex, an area including portions of both medial and inferior occipital gyrus (BA 18, 19), was more active for visual form recognition. Additional areas included the caudal portions of the medial and inferior temporal gyrus (BA 37) and discrete regions in the parahippocampal gyrus (BA 20/36). Preferential activation for visual form recognition was also observed in the left inferior parietal cortex (BA 39) and IPS. In the frontal cortex, left side activation was seen in the inferior frontal cortex, including the caudal portion of the inferior frontal gyrus (BA 44, 45) and possibly also a small portion of the adjoining medial frontal gyrus (BA 46).

TABLE I. Loci of common activation in the two task conditions[a]

Region[b]	Brodman's Area	Talairach coordinates		
		x	y	z
Occipitotemporal				
Cuneous,[c] B	17	1	−82	−3
Middle occipital gyrus,[c] B	19	−25	−82	−18
Inferior occipital gyrus,[c] B	18, 19	28	−85	5
Lingual and fusiform gyrus,[c] B	19, 37	36	−61	9
Middle and inferior temporal gyrus,[c] B	37	39	−55	1
Superior temporal gyrus, R	22	−48	−39	−18
Parietal				
Intraparietal sulcus[c] and adjoining cortices, B	7, 40, 39	−25	−51	−44
Precuneous	7b	0	−61	−55
Frontal				
Medial superior frontal gyrus, SMA/preSMA, L	6	1	5	−52
Cingulate sulcus, L	6, 32	1	9	−48
Cingulate gyrus, R	24, 32	−9	19	−25
Superior and middle frontal gyrus,[c] PMd B	6	−20	6	−55
Lateralprecentral sulcus,[c] B	6, 8, 9, 44	−41	7	−37
Inferior frontal sulcus,[c] B	44, 45, 46, 9	46	22	−25
Insula, B		−36	19	1
Cerebellum				
Lateral, B		−29	−62	20
Medial, L		12	−73	24

[a] Sign convention of the coordinates is that left, anterior, and inferior are positive. Multiple Brodmann regions are sometimes listed for a single Talairach coordinates to indicate the proximity to the intersection of those regions.

[b] B = bilateral activation. The activation is relatively symmetric, but the side with more robust activation is listed. L = left hemisphere; R = right hemisphere.

[c] Activation in these loci is not well localized; see text and figures for more complete information.

In the medial wall, a locus at the preSMA/cingulate region was also more active during visual recognition (BA 6, 32). Additionally, a region in the left cerebellum was also more active.

In both the occipital temporal (comparing images z = 5, 9, 12, in Figs. 2 and 3) and inferior frontal regions (comparing images z = −22, −18, −14, −10 in Figs. 2 and 3), areas that were more active during the visual form recognition task were more ventral and anterior to the regions that were commonly activated by both tasks.

Activation for spatial recognition was observed mostly in the right hemisphere. There was activation in the right fusiform gyrus (BA 37), the bilateral superior parietal lobule (BA 7b), right superior occipital cortex (BA 19), right lateral precentral cortex (BA 4), right superior frontal sulcus (BA 6, 8), right postcentral sulcus, left frontal pole (BA 10), and anterior cingulate gyrus (BA 24, 32). Additionally, the left caudate/putaman was more active in the spatial recognition task.

To make sure that the observed hemispheric laterality was not just an artifact of thresholding in the analysis, another test was carried out. Slices with z coordinate between −52 and −24, inclusive, were selected to test the laterality in the spatial recognition condition, and slices with z coordinate between −59 and 24, inclusive, were selected to test the laterality in the visual recognition condition. A laterality index, defined as the weighted average t value of all voxels in each volume, was then computed for each subjects (Table 3; see Methods). The results indicate consistency with the group response in Figure 2, with the most consistent response being right hemispheric dominance in spatial recognition and left hemispheric dominance in visual recognition. However, significant inter subject difference was also revealed. Although visual form recognition consistently evoked left-dominant activation, the right hemispheric dominance in the spatial recognition condition appears to be a weak result.

In addition to brain regions that showed a positive BOLD response in both tasks, a number of brain regions also showed a negative BOLD response. These regions lie mostly in the medial wall, including the posterior portion of medial SMA (BA6), the portion of cingulate gyrus lying immediately beneath it and
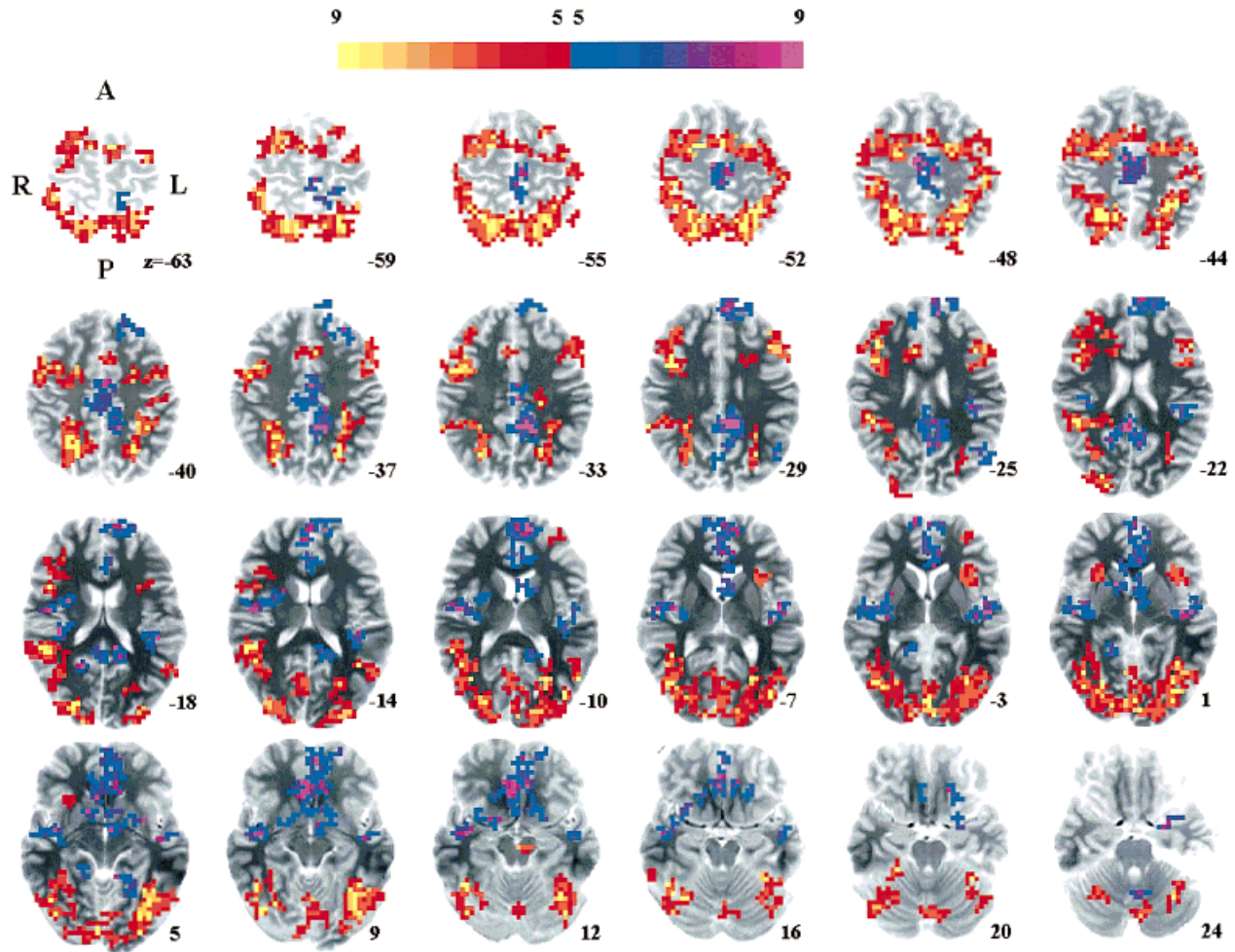
Figure 2.

Brain loci commonly activated in both task conditions. Activation maps from all subjects were superimposed and displayed in Talairach coordinates. The z coordinate for each slice is also indicated. Cortical regions exhibiting positive BOLD responses are labeled with the color red through yellow. Hotter color indicates higher degree of reproducibility among the subjects, as indicated by the color-coded bar at the top of the figure. Pixels depicted were thus reproduced in 5/9 subjects to 9/9 subjects. Pixels that were activated in less than 5/9 subjects are not included. Cortical regions exhibiting negative BOLD response in both tasks are labeled with colors blue through purple. Again, higher color temperature indicates higher reproducibility among the subjects.

extending to the caudal end of the gyrus (BA 24, 31), the medial wall of the anterior portion of the superior frontal gyrus (BA 9), and the frontal pole (BA 10). Bilateral deactivation was also observed in the posterior portion of the insula and the adjacent cortex of the superior temporal gyrus (Fig. 2).

DISCUSSION

The current study was designed to eliminate a number of potentially confounding factors that existed in previous studies that directly contrasted visual processing of spatial and object information. Visual information processing was restricted to the level of visual feature analysis [Ullman, 1989], thereby eliminating the memory process associated with face or object recognition. Motor responses were eliminated from the stimulus display period to prevent central activation associated with limb movement control. Eye movement was better controlled and more balanced in the two tasks by using identical stimuli for the two tasks and by presenting the small stimuli briefly, one at a time [Hallett and Lightstone, 1976]. Still, many brain processes were involved in performing the tasks, as reflected in the complex patterns of the observed BOLD response.
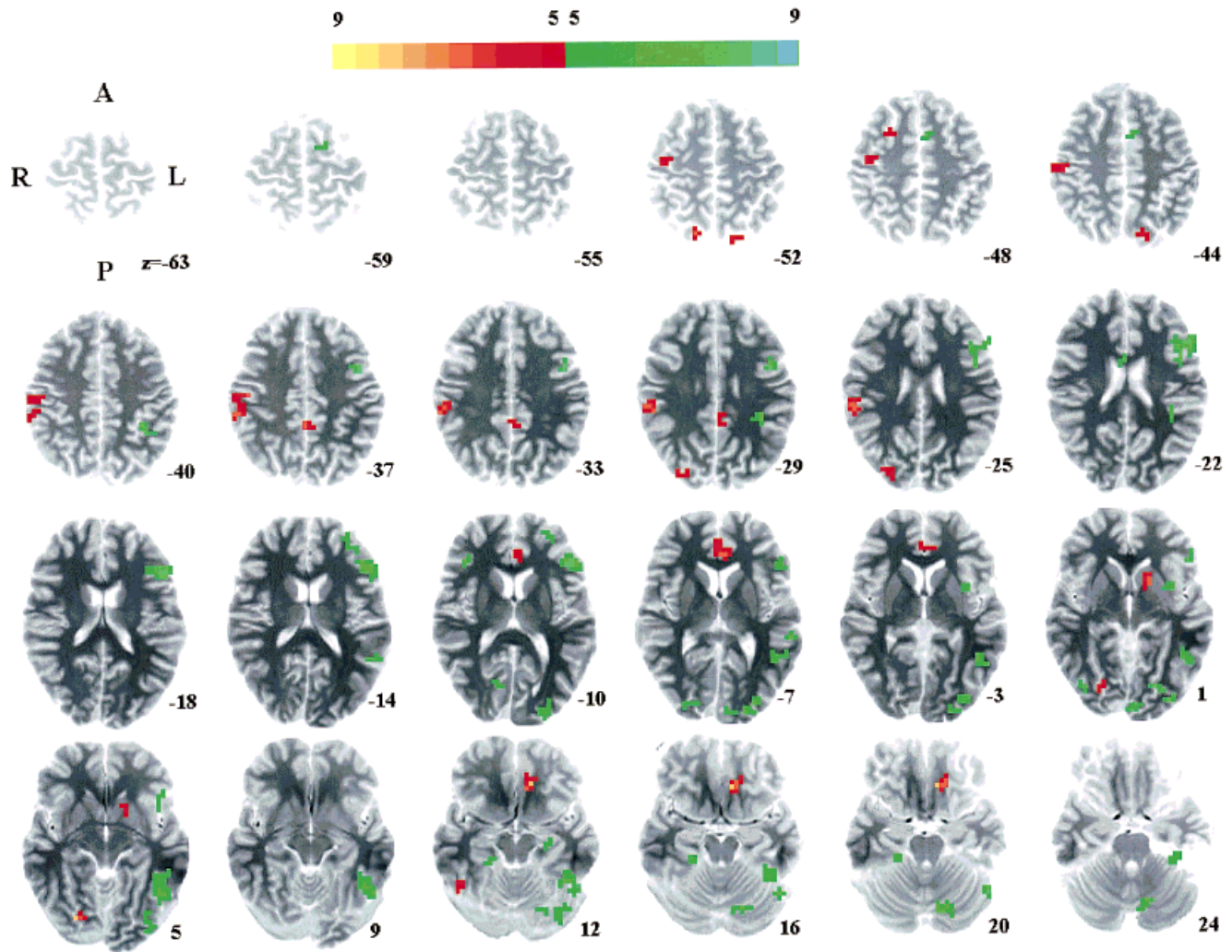
Figure 3.

Brain loci that were differentially activated in the two task conditions. Again, activation maps from all subjects are superimposed and displayed in Talairach coordinates. Cortical loci that are more active in spatial perception than in visual form perception are labeled in red; cortical loci that are more active in visual form perception are labeled in green. Only pixels reproducible in more than 5/9 subjects were included.

During task performance, as opposed to the periods in which only visual fixation of the cross hair at the center of the screen was required, a number of mental processes become either engaged or more active. These include, but are not limited to, processing visual and spatial information, encoding and retrieval of information in working memory, directing attention to different locations in space, and eye movement control. Consequently, positive BOLD responses during task performance were observed in both the posterior and frontal cortices. The activation of the primary visual cortex, the lateral occipital region, including the occipital temporal junction, the fusiform and lingual gyri in the basal part of the brain, are consistent with the current understanding of these regions being involved in general visual processing, including contour extraction [Reppas et al., 1997], intermediate feature processing [Malach et al., 1995], detection of coherent visual structure information [Schacter et al., 1995], and possibly object and face recognition [Haxby et al., 1996; Kanwisher et al., 1997; Sergent et al., 1992]. The function served by the activity in the right superior temporal gyrus is less clear. This region is part of the temporo-parieto-occipital association area and is thought to play an important role in integrating sensory information from multiple modalities [Pearlson, 1997]. The strong bilateral activation of the superior and inferior parietal cortex has been implicated in both

TABLE II. Brain regions exhibiting significantly different BOLD responses
in the two tasks

Region[a]	Brodman's Area	Talairach coordinates		
		x	y	z
More active in visual form recognition				
Occipitotemporal				
Middle occipital gyrus, L	18, 19	31	−85	−3
Middle/inferior temporal gyrus, L	21, 37	49	−53	5
Fusiform gyrus, L	37	38	−44	12
Parahippocampal gyrus, B	36, 20	−23	−29	16
Lingual gyrus, L	18	2	−90	1
Superior temporal gyrus, L	22	59	−33	−7
Parietal				
Intraparietal sulcus, L		32	−37	−40
Frontal				
Medial superior frontal gyrus, preSMA, L	6	02	9	−44
Superior frontal sulcus, L	6	12	6	−59
Insula, L		32	7	1
Inferior frontal region, L	44, 45	50	23	−18
	46, 10	29	54	−10
Cerebellum				
Medial, L		16	−72	20
More active in visual spatial recognition				
Occipitotemporal				
Fusiform/inferior occipital gyrus, R	37	−46	−51	12
Superior occipital gyrus, R	19	−29	−80	−25
Parietal				
Postcentral sulcus, R		−56	−27	−29
Superior parietal lobule, B	7b	−16	−66	−52
L		12	−71	−44
Cingulate gyrus	31	3	−40	−33
Frontal				
Superior frontal gyrus, R	6	−25	12	−48
Central sulcus, R		−53	−16	−40
Frontal orbital gyrus, L	25	10	27	16
Frontal cingulate gyrus	24, 32	1	37	−7
Deep nucleus				
Caudate/putaman, L		15	11	1

[a] B = bilateral activation; L = left hemisphere; R = right hemisphere.

perceptual and motor functions [Andersen, 1997; Sakata et al., 1997], including attention shifting [Corbetta et al., 1995], spatial processing for eye movement [Corbetta, 1998], limb movement and grasp control [Rizzolatti et al., 1996], motor imagery [Grafton et al., 1996], and perception of 3D structure [Layman and Greene, 1988]. The activation of the dorsal lateral frontal cortex and in the inferior frontal gyrus is consistent with the explicit short-term memory component in the present task [Cohen et al., 1997; Courtney et al., 1997].

The activation observed here may be partially accounted for by eye movement, but eye movement per se is unlikely to account for all the activation. Strong parietal activation was also observed in a study in which eye movement was minimized [Le et al., 1998]. In monkeys, cooling of the intraparietal sulcus region has been shown to induce no gross deficit in delayed or nondelayed saccadic eye movements, indicating the nonessential role played by this region in eye movement [Chafee and Goldman-Rakic, 1998; Goldman-Rakic and Chafee, 1994]. In the dorsal and medial frontal cortex, the areas activated are generally regarded as serving some sort of motor association or motor preparation functions, hence the name ''premotor cortex'' [Shen and Alexander, 1997; Picard and

TABLE III. Hemispheric laterality in spatial and visual recognition conditions[a]

Subject	Spatial recognition		Visual recognition	
	Laterality-index (variance)	Dominance (significant level)	Laterality-index (variance)	Dominance (significant level)
1	0.006 (0.047)	none	0.024 (0.035)	none
2	−0.311 (0.074)	R($P < 0.0005$)	0.364 (0.037)	L($P < 0.0005$)
3	−0.270 (0.085)	R($P < 0.0005$)	0.599 (0.027)	L($P < 0.0005$)
4	0.333 (0.077)	L($P < 0.0005$)	−0.149 (0.031)	R($P < 0.0005$)
5	0.192 (0.094)	L($P < 0.025$)	0.272 (0.041)	L($P < 0.0005$)
6	−0.090 (0.061)	none	0.025 (0.034)	none
7	0.504 (0.061)	L($P < 0.0005$)	0.088 (0.064)	none
8	−0.266 (0.048)	R($P < 0.0005$)	0.376 (0.033)	L($P < 0.0005$)
9	−0.207 (0.074)	R($P < 0.005$)	0.165 (0.028)	L($P < 0.0005$)

[a] Note that the hemispheric dominance is labeled as insignificant when the corresponding P value is greater than 0.05. R = right hemisphere; L = left hemisphere.

Strick, 1996; Wise et al., 1996]. Nevertheless, these regions were reliably activated in the present task, with the exception of the primary motor cortex, which indicated the functional specificity of this region in controlling *actual* limb movements. Two loci in the frontal cortex have been associated with eye movement control, the supplementary eye field on the medial wall and the frontal eye field on the lateral surface. The frontal eye field is generally believed to be either in BA6 or BA4 near the caudal end of the superior frontal sulcus [Luna et al., 1998; Petit et al., 1997]. Eye movements could, therefore, account for portions of the activation observed, but do not seem to be a sufficient explanation for the strong activation in the dorsal premotor region. Another potential contributing factor may be motor preparation [Richter et al., 1997]. However, preparatory activity has so far been observed only when prompt motor action is required following some sort of cue stimulus, and the subjects

TABLE IV. Brain regions exhibiting negative BOLD response in both tasks

Region[a]	BA	Talairach coordinates		
		x	y	z
Lingual/fusiform gyrus, L	19, 30	22	−52	5
Insula/superior temporal gyrus, B	22	48	−8	−3
Precuneous, L	7b, 31, 23	10	−45	−32
Cingulate gyrus,* B	24	1	−16	−44
Frontal cingulate gyrus,* B	32, 10, 24	9	45	9

[a] B = bilateral activation; L = left hemisphere.
*Activation in these loci is not well localized.

therefore need to be "prepared." Such requirement did not exist in this study. It is, therefore, unlikely that motor preparation contributed significantly to the observed activation.

It has been argued that activation of the lateral cerebellum in paradigms that do not require overt movements [Allen et al., 1997], or in which activation due to movements has been subtracted out [Kim et al., 1994; Le, 1998], is due to nonmotor, cognitive functions served by the cerebellum. However, the activation of the entire premotor structure in the current perceptual task with no concurrent motor response and the similarity of the parietal and frontal activation to those observed in motor paradigms [Inoue et al., 1998; Lacquaniti et al., 1997] make it hard to ignore the alternative possibility that action and perception are phylogenetically strongly coupled, and visual perceptual tasks activate structures for action preparation, including the cerebellum, by default. This is not to say that the cerebellum is involved only in controlling movement, as evidence of the cerebellum performing nonmotor functions is quite compelling [Ivry, 1993], but that cerebellar activation in visual perceptual tasks may not necessarily imply an essential role in task performance.

When BOLD signals from the two tasks are compared, the resulting patterns of activation show a number of distinct features. First, the activation is smaller and more discrete, compared to the common activation in both tasks, suggesting that many of the same processes are involved in performing the two tasks. Additionally, it is possible that the observed differential activation may have been further reduced due to automatic activation in both tasks of cortical

structures involved in visual form and spatial processing and is only slightly modulated by task requirements and the subject's conscious attention. Psychophysical studies have showed that visual object and word recognition is automatic in the sense that they occur even when subjects are engaged in another simultaneous task while trying to avoid recognizing the object or words [Dunbar and MacLeod, 1984; Frith et al., 1995; Glaser and Dungelhoff, 1984].

Second, there is as much a left-right segregation as there is a dorsal-ventral segregation of the differential activation in the grouped response. The tendency for visual form recognition to preferentially activate the ventral-left part of the brain was further confirmed in an explicit laterality test on data from individual subject. The criteria for this last test were designed to be substantially different from the original test in which the laterality was first revealed. This was done to make sure that the observed hemispheric laterality was not just a thresholding artifact. The results of the test were not expected to follow the grouped response in Figure 3 in any quantitative sense, as the criterion for voxel inclusion was quite different in the two cases. Nevertheless, the results were consistent qualitatively.

The difference of the two tasks by design is that for visual form recognition, subjects pay attention to object pattern and engage working memory to store and retrieve the pattern for comparison, and that for visual spatial recognition, they pay attention to spatial information and engage spatial working memory. Accordingly, the left-inferior frontal activation in this study may reflect the mediation of working memory for visual form information by this region. Assuming that the "central executive" component of the working memory hypothesis is common to both tasks and that the "visual sketch pad" component is not, the results further suggest that the former component resides in the dorsal lateral frontal cortex and the latter in the inferior frontal gyrus. The hemispherical laterality may result from the symbolic or linguistic encoding of visual form information. This, however, does not necessarily negate our conclusions above, as symbolic or linguistic encoding is likely an integral part of object working memory. Activation in this latter region has been observed in paradigms involving face recognition, except that it is usually stronger in the right hemisphere than in the left hemisphere [Courtney et al., 1996; Haxby et al., 1994]. The activation of this region is consistent with anatomical evidence from nonhuman primates that this region receives strong input from the inferior temporal region [Boussaoud et al., 1995] and is, therefore, a part of the pathways that

process visual form information and associate visual form information with action.

To the extent that areas in the lateral occipital and occipitotemporal cortices are preferentially activated in visual form processing, the results presented here are consistent with results from PET studies that contrasted face recognition with spatial recognition [Courtney et al., 1996; Haxby et al., 1991; Haxby et al., 1994]. The difference is that face recognition has tended to elicit bilateral activation, whereas the activation seen in this study is mostly in the left hemisphere, more consistent with the PET result in which object rather than face recognition was contrasted with spatial recognition [Kohler et al., 1995]. The site of activation for visual form recognition in this study seems to correspond more closely with the site for face recognition in fMRI studies than to the site labeled for object recognition [Kanwisher et al., 1997]. The activation in the lateral occipitotemporal region also seems to reside mostly in the caudal portion of the middle and inferior temporal gyri, anterior to MT and the lateral occipital (LO) region proposed for visual form processing in a previous fMRI study [Malach et al., 1995]. Nevertheless, it is still possible that area LO is relatively specific for visual form processing, except that the processing in this region is highly automatic and is not significantly influenced by attention. Areas commonly activated by both tasks do include area LO.

There may be multiple factors contributing to the observed left-dominant activation in visual form recognition. One of these may be the linguistic or symbolic coding of visual information. Over half of the subjects appeared to ascribe some sort of names to the visual patterns. Presumably the names would be more facilitative for the visual pattern recognition task than for the visual spatial task, although concrete evidence is lacking in this regard. This would also be consistent with observations that letter strings evoke left-dominant activation when compared with simple textures [Puce et al., 1996]. The dynamics of activation in an experimental run may also contribute to the observed left-dominance. In a PET study that contrasted face working memory with a sensory motor control, it was found that there was predominant left hemisphere activation for longer delays [Haxby et al., 1995]. The hypothesis advanced was that the left hemisphere contained a more "analyzed" version of faces and, therefore, could be retained in the memory for a longer time. A related observation on the dynamics of activation pattern was made in a texture perception PET study [Beason-held et al., 1998], in which the initial right occipital-temporal dominant activation to textures composed of local features diminished over

repeated runs. The observed left hemisphere dominance in visual pattern recognition in this study could also result from these kinds of dynamics, as the length of the runs in this study was much longer than those in the two PET studies mentioned above.

The activation on the left side of the medial wall lies within the putative human homology of the medial premotor areas in monkeys. This region is active in a diverse set of visually instructed motor tasks as well as word association tasks [Picard and Strick, 1996]. The exact functional roles of this region have not been well defined. Although this region is generally regarded as serving some sort of motor function, neurons coding object-centered information also have been observed in this region in primates [Olson and Gettner, 1995, 1996]. Part of the activation in this region thus might serve to associate object information with potential actions. This would explain why there is a locus in this region that is more active in visual form recognition than in spatial recognition.

Aside from the activation loci in the cingulate gyrus and left caudate/putamen, visual spatial recognition preferentially activated loci in the right hemisphere. The locations of these sites are in good agreement with a recent PET study except for the difference in laterality [Courtney et al., 1996]. To the extent that the dorsal premotor region is preferentially more active in the spatial task, the results are consistent with the suggestion that this region is specialized for spatial working memory [Courtney et al., 1998]. However, the most reproducible preferential activation seems to reside in the anterior-inferior parietal cortex and the adjacent lateral central sulcus region.

Areas in which neural activity was suppressed during task performance lie mostly along the medial wall. The deactivation of these regions is probably due in part to the brain's need to conserve resources—brain structures not relevant for performing the task simply receive less blood than active structures. However, the deactivation may also serve a functional purpose. Blood flow to the posterior and frontal cingulate gyrus for the limbic system is suppressed during task performance, probably so that emotional responses would not get in the way of processing of visual information [Mega et al., 1997]. Suppression of auditory input also helps one to concentrate on visual input and other mental functions [Haxby et al., 1994].

CONCLUSIONS

Results from this study reveal that attending to visual stimuli in the environment activates a system of pathways involving not only the visual areas in the posterior cortex, but also areas in the frontal cortex that are presumably related to the preparation of actions, as well as the cerebellum. Focusing attention on specific attributes of the visual stimuli modulates the activity of neural structures in the pathways. The direction of the modulation is consistent with the hypothesis that visual spatial processing occurs in the dorsal pathway and that visual form processing occurs in the ventral pathway. However, hemispheric modulation in the two task conditions is equally prominent. The left hemisphere is consistently more active in the visual form recognition task, suggesting that the left hemisphere plays a more dominant role in the encoding and manipulation of visual form information in most people.

REFERENCES

Allen G, Buxton RB, Wong EC, Courchesne E. 1997. Attentional activation of the cerebellum independent of motor involvement. Science 275:1940–1943.

Andersen RA. 1997. Multimodal integration for the representation of space in the posterior parietal cortex. Philos Trans R Soc Lond B Biol Sci 352:1421–1428.

Beason-held LL, Purpura KP, van Meter JW, Azari NP, Mangot DJ, Optican LM, Mentis MJ, Alexander GE, Grady CL, Horwitz B, Rapoport SI, Schapira MB. 1998. PET reveals occipitotemporal pathway activation during elementary form perception in humans. Visual Neurosci 15:503–511.

Boussaoud D, di Pellegrino G, Wise SP. 1995. Frontal lobe mechanisms subserving vision-for-action versus vision-for-perception. Behav Brain Res 72:1–15.

Chafee MV, Goldman-Rakic PS. 1998. Matching patterns of activity in primate prefrontal area 8a and parietal area 7ip neurons during a spatial working memory task. J Neurophysiol 79:2919–2940.

Chen W, Zhu XH. 1997. Suppression of physiological eye movement artifacts in functional MRI using slab presaturation. Magn Reson Med 38:546–550.

Clark VP, Keil K, Maisog JM, Courtney S, Ungerleider LG, Haxby JV. 1996. Functional magnetic resonance imaging of human visual cortex during face matching: a comparison with positron emission tomography. Neuroimage 4:1–15.

Cohen JD, Perlstein WM, Braver TS, Nystrom LE, Noll DC, Jonides J, Smith EE. 1997. Temporal dynamics of brain activation during a working memory task [see comments]. Nature 386:604–608.

Corbetta M. 1998. Frontoparietal cortical networks for directing attention and the eye to visual locations: identical, independent, or overlapping neural systems? Proc Natl Acad Sci USA 95:831–838.

Corbetta M, Shulman GL, Miezin FM, Petersen SE. 1995. Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. Science 270:802–805.

Courtney SM, Petit L, Maisog JM, Ungerleider LG, Haxby JV. 1998. An area specialized for spatial working memory in human frontal cortex. Science 279:1347–1351.

Courtney SM, Ungerleider LG, Keil K, Haxby JV. 1996. Object and spatial visual working memory activate separate neural systems in human cortex. Cereb Cortex 6:39–49.

Courtney SM, Ungerleider LG, Keil K, Haxby JV. 1997. Transient and sustained activity in a distributed neural system for human working memory [see comments]. Nature 386:608–611.

Dunbar K, MacLeod CM. 1984. A horse race of a different color: Stroop interference patterns with transformed words. J Exp Psychol Hum Percept Perform 10:622–639.

Farah MJ. 1990. Visual Agnosia: Disorders of Object Recognition and What They Tell Us about Normal Vision. Cambridge: MIT Press.

Frith CD, Kapur N, Friston KJ, Liddle PF, Frackowiak RSJ. 1995. Regional cerebral activity associated with incidental processing of pseudo-words. Hum Brain Map 3:153–160.

Glaser WR, Dungelhoff FJ. 1984. The time course of picture-word interference. J Exp Psychol Hum Percept Perform 10:640–654.

Goldman-Rakic PS, Chafee MV. 1994. Feedback processing in prefrontal-parietal circuits during memory-guided saccades. Soc Neurosci Abs 20:335.2.

Goodale MA, Milner AD. 1992. Separate visual pathways for perception and action. Trends Neurosci 15:20–25.

Grafton ST, Arbib MA, Fadiga L, Rizzolatti G. 1996. Localization of grasp representations in humans by positron emission tomography: 2. observation compared with imagination. Exp Brain Res 112:103–111.

Hallett PE, Lightstone AD. 1976. Saccadic eye movements to flashed targets. Vision Res 16:107–114.

Haxby JV, Grady CL, Horwitz B, Ungerleider LG, Mishkin M, Carson RE, Herscovitch P, Schapiro MB, Rapoport SI. 1991. Dissociation of object and spatial visual processing pathways in human extrastriate cortex. Proc Natl Acad Sci USA 88:1621–1625.

Haxby JV, Horwitz B, Ungerleider LG, Maisog JM, Pietrini P, Grady CL. 1994. The functional organization of human extrastriate cortex: a PET-rCBF study of selective attention to faces and locations. J Neurosci 14:6336–6353.

Haxby JV, Ungerleider LG, Horwitz B, Rapoport SI, Grady CL. 1995. Hemispheric difference in neural systems for face working memory: a PET-rCBF study. Hum Brain Mapp 3:68–82.

Haxby JV, Ungerleider LG, Horwitz B, Maisog JM, Rapoport SI, Grady CL. 1996. Face encoding and recognition in the human brain. Proc Natl Acad Sci USA 93:922–927.

Inoue K, Kawashima R, Satoh K, Kinomura S, Goto R, Koyama M, Sugiura M, Ito M, Fukuda H. 1998. PET study of pointing with visual feedback of moving hands. J Neurophysiol 79:117–125.

Ivry R. 1993. Cerebellar involvement in the explicit representation of temporal information. Ann NY Acad Sci 682:214–230.

Kanwisher N, McDermott J, Chun MM. 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci 17:4302–4311.

Kim SG, Ugurbil K, Strick PL. 1994. Activation of a cerebellar output nucleus during cognitive processing. Science 265:949–951.

Kohler S, Kapur S, Moscovitch M, Winocur G, Houle S. 1995. Dissociation of pathways for object and spatial vision: a PET study in humans. Neuroreport 6:1865–1868.

Lacquaniti F, Perani D, Guigon E, Bettinardi V, Carrozzo M, Grassi F, Rossetti Y, Fazio F. 1997. Visuomotor transformations for reaching to memorized targets: a PET study. Neuroimage 5:129–146.

Layman S, Greene E. 1988. The effect of stroke on object recognition. Brain Cogn 7:87–114.

Le THPJV, Hu X. 1998. 4 T-fMRI study of nonspatial shifting of selective attention. J Neurophysiol 1535–1548.

Luna B, Thulborn KR, Strojwas MH, McCurtain BJ, Berman RA, Genovese CR, Sweeney JA. 1998. Dorsal cortical regions subserving visually guided saccades in humans: an fMRI study. Cereb Cortex 8:40–47.

Malach R, Reppas JB, Benson RR, Kwong KK, Jiang H, Kennedy WA, Ledden PJ, Brady TJ, Rosen BR, Tootell RB. 1995. Object-related activity revealed by functional magnetic resonance imaging in human occipital cortex. Proc Natl Acad Sci USA 92:8135–8139.

Mega MS, Cummings JL, Salloway S, Malloy P. 1997. The limbic system: an anatomic, phylogenetic, and clinical perspective. J Neuropsychiatry Clin Neurosci 9:315–330.

Oldfield RC. 1971. The assessment of and analysis of handedness: the Edinburgh Inventory. Neuropsychologia 97–113.

Olson CR, Gettner SN. 1995. Object-centered direction selectivity in the macaque supplementary eye field. Science 269:985–988.

Olson CR, Gettner SN. 1996. Representation of object-centered space in the primate frontal lobe. Brain Res Cogn Brain Res 5:147–156.

Pearlson GD. 1997. Superior temporal gyrus and planum temporale in schizophrenia: a selective review. Prog Neuropsychopharmacol Biol Psychiatry 21:1203–1229.

Petit L, Clark VP, Ingeholm J, Haxby JV. 1997. Dissociation of saccade-related and pursuit-related activation in human frontal eye fields as revealed by fMRI. J Neurophysiol 77:3386–3390.

Picard N, Strick PL. 1996. Motor areas of the medial wall: a review of their location and functional activation. Cereb Cortex 6:342–353.

Puce A, Allison T, Asgari M, Gore JC, McCarthy G. 1996. Differential sensitivity of human visual cortex to faces, letterstrings and textures: a functional magnetic resonance imaging study. J Neurosci 16:5205–5215.

Reppas JB, Niyogi S, Dale AM, Sereno MI, Tootell RB. 1997. Representation of motion boundaries in retinotopic human visual cortical areas. Nature 388:175–179.

Richter W, Anderson PM, Georgopoulos AP, Kim SG. 1997. Sequential activity in human motor areas during a delayed cued finger movement task studied by time-resolved fMRI. Neuroreport 8:1257–1261.

Rizzolatti G, Fadiga L, Matelli M, Bettinardi V, Paulesu E, Perani D, Fazio F. 1996. Localization of grasp representations in humans by PET: 1. observation versus execution. Exp Brain Res 111:246–252.

Sakai K, Hikosaka O, Miyauchi S, Takino R, Sasaki Y, Putz B. 1998. Transition of brain activation from frontal to parietal areas in visuomotor sequence learning. J Neurosci 18:1827–1840.

Sakata H, Taira M, Kusunoki M, Murata A, Tanaka Y. 1997. The TINS lecture: the parietal association cortex in depth perception and visual control of hand action. Trends Neurosci 20:350–357.

Schacter DL, Reiman E, Uecker A, Polster MR, Yun LS, Cooper LA. 1995. Brain regions associated with retrieval of structurally coherent visual information. Nature 376:587–590.

Sergent J, Ohta S, MacDonald B. 1992. Functional neuroanatomy of face and object processing: a positron emission tomography study. Brain 115:15–36.

Shen L, Alexander GE. 1997. Preferential representation of instructed target location versus limb trajectory in dorsal premotor area. J Neurophysiol 77:1195–1212.

Strupp JP. 1996. Stimulate: AGUI based fMRI analysis software package. Neuroimaging 3:S607.

Talairach J, Tournoux P. 1988. Co-Planar Stereotaxic Atlas of the Human Brain Trans. New York: Thieme.

Ullman S. 1989. Aligning pictorial descriptions: an approach to object recognition. Cognition 32:193–254.

Ungerleider LG, Mishkin M. 1982. Two cortical pathways. In: Ingle DJ, Goodale MA, Mansfield RJW (eds): Analysis of Visual Behavior. Cambridge: MIT Press, pp 549–586.

Wise SP, di Pellegrino G, Boussaoud D. 1996. The premotor cortex and nonstandard sensorimotor mapping. Can J Physiol Pharmacol 74:469–482.

Woods RP, Grafton ST, Holmes CJ, Cherry SR, Mazziotta JC. 1998. Automated image registration: I. general methods and intrasubject, intramodality validation. J Comput Assist Tomogr 22:139–152.

Yarbus AL. 1967. Eye Movements and Vision. New York: Plenum Press.