

Topographical Layout of Hand, Eye, Calculation, and Language-Related Areas in the Human Parietal Lobe

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Summary

To identify subdivisions of the human parietal cortex, we collected fMRI data while ten subjects performed six tasks: grasping, pointing, saccades, attention, calculation, and phoneme detection. Examination of task intersections revealed a systematic anterior-to-posterior organization of activations associated with grasping only, grasping and pointing, all visuomotor tasks, attention and saccades, and saccades only. Calculation yielded two distinct activations: one unique to calculation in the bilateral anterior IPS mesial to the supramarginal gyrus and the other shared with phoneme detection in the left IPS mesial to the angular gyrus. These results suggest human homologs of the monkey areas AIP, MIP, V6A, and LIP and imply a large cortical expansion of the inferior parietal lobule correlated with the development of human language and calculation abilities.

Introduction

Parietal cortex is active during a variety of visuospatial tasks, including hand reaching, grasping, eye and/or attention orienting, mental rotation, and spatial working memory (Culham and Kanwisher, 2001). However, other tasks without obvious visuospatial requirements, such as mental calculation (Dehaene et al., 1999) or phonological word processing (Jonides et al., 1998) also yield parietal activations, sometimes at very similar locations. One possible interpretation of these findings is that the parietal cortex is involved in abstract and generic processes that are useful for many tasks. In support of this possibility, Wojciulik and Kanwisher (1999) have observed overlapping activations in the parietal lobe in a variety of tasks that all shared an abstract component of attention orienting. According to this interpretation, the parietal activation during calculation, in particular, would reflect the engagement of generic mechanisms of coordinate transformation and attention (Zago et al., 2001).

An alternative possibility, however, is that the human intraparietal sulcus consists of a mosaic of distinct specialized areas, including a region for the manipulation of numerical quantities (Dehaene and Cohen, 1995; Dehaene et al., 1998). This fine-grained anatomical special-

ization might be masked by interindividual variability and the lack of anatomical precision inherent in comparing group studies from different neuroimaging laboratories. In support of this possibility, neurophysiological studies in monkeys have revealed a parcellation of the parietal lobe into several specialized areas whose neurons exhibit distinct response properties (Rizzolatti et al., 1998). Furthermore, neuroimaging studies have also begun to reveal functional specialization in the human parietal lobe, for instance, hand versus eye movement (Kawashima et al., 1996) or grasping versus pointing (Grafton et al., 1996).

The aim of the present study is to further characterize the functional organization of the human parietal lobe. We collected functional magnetic resonance images while subjects performed six different tasks: pointing, grasping, attention orienting, saccades, calculation, and phoneme detection. We did not design new tasks, but rather, replicated and extended existing tasks in order to identify all six task-related activations within a subject in a few minutes. This allowed us to examine the geometrical relations of those activations. In particular, we examined the overlap between the areas engaged in calculation and in visuospatial tasks. The use of simple grasping, pointing, and saccades tasks allowed us to identify putative human equivalents of monkey parietal areas and to locate the human activations during calculation and language tasks relative to those functional landmarks.

Results

In each task, a large network comprising parietal, lateral frontal, and mesial frontal regions was observed. We first describe the global pattern of activation observed in each task relative to its control (Table 1 and Figure 1). Focusing on parietal activations, we then describe which active regions, if any, were selectively activated by a single task (Table 2 and Figure 2). Finally, we consider parietal regions that were common to two or more tasks (Table 3 and Figure 2).

Activations Observed in Each Task

Grasping

As expected, given that the task involved right hand movements, a unilateral activation of the left central sulcus was observed in the hand region of the motor homunculus. In addition, grasping activated the frontal and parietal regions. The frontal network included a bilateral mesial superior frontal gyrus activation in the vicinity of the supplementary motor area extending into the anterior cingulate gyrus. There was also a left precentral gyrus activation extending anteriorly into the middle frontal gyrus. In the inferior frontal gyrus (BA 44), a bilateral activation was observed. The parietal network contained a unilateral left postcentral activation facing the central sulcus activation. In addition, there were bilateral activations in the anterior part of the supramarginal gyrus, the postcentral sulcus, the horizontal seg-

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Table 1. Areas Activated during Each of the Six Primary Tasks Relative to Their Respective Controls

Task	Anatomical Region	Talairach Coordinates			T Values	
Calculation	Left superior frontal gyrus	-8	8	52	5.53	
	Right superior frontal gyrus	4	32	52	7.19	
	Left middle frontal gyrus	-28	-8	60	4.76	
	Left middle frontal gyrus	-36	-56	28	5.80	
	Left middle frontal gyrus	-28	0	56	5.89	
	Left middle frontal gyrus	-44	32	28	5.39	
	Left middle frontal gyrus	-44	56	12	3.91	
	Left inferior frontal gyrus	-56	12	28	8.51	
	Right inferior frontal gyrus	44	20	24	4.57	
	Right inferior frontal gyrus	52	8	12	4.57	
	Left cingular gyrus	-8	24	28	4.34	
	Right cingular gyrus	4	24	32	5.36	
	Left orbital gyrus	-32	28	0	3.27	
	Right orbital gyrus	36	24	0	4.69	
	Left postcentral gyrus	-48	-4	52	7.45	
	Left IPS posterior segment	-32	-72	52	4.78	
	Right IPS posterior segment	32	-60	44	3.65	
	Left inferior parietal lobule	-12	-72	48	3.22	
	Left supramarginal gyrus	-60	-32	44	3.78	
	Left angular gyrus	-36	-64	36	4.44	
	Left anterior putamen	-28	12	0	4.43	
	Right anterior putamen	16	8	8	5.01	
	Left insula	-40	16	0	4.11	
	Language	Left superior frontal gyrus	-4	12	56	11.33
		Left inferior frontal gyrus	-56	20	32	6.42
		Left inferior frontal gyrus	-44	16	12	5.85
		Right inferior frontal gyrus	52	16	8	5.33
		Left precentral gyrus	-52	0	48	5.29
Left supramarginal gyrus		-64	-36	36	4.46	
Left angular gyrus		-28	-80	40	7.90	
Saccades	Left superior frontal gyrus	-8	8	48	6.87	
	Left superior frontal gyrus	-24	-4	68	5.06	
	Right superior frontal gyrus	4	4	56	7.26	
	Left middle frontal gyrus	-36	0	56	7.42	
	Right middle frontal gyrus	28	-4	56	8.25	
	Right precentral gyrus	60	8	32	4.33	
	Left superior parietal lobule	-16	-80	48	9.93	
	Right superior parietal lobule	16	-72	56	10.34	
	Right IPS horizontal segment	40	-48	48	4.78	
	Left precuneus	-4	-60	56	10.77	
	Right precuneus	8	-80	44	6.00	
	Left IPS posterior segment	-24	-84	40	7.64	
	Right IPS posterior segment	20	-76	40	7.32	
	Left IPTO	-8	-88	36	5.73	
	Right IPTO	8	-84	32	4.95	
	Right anterior putamen	20	8	4	4.58	
	Left thalamus	-16	-24	12	4.39	
	Grasping	Left superior frontal gyrus	-16	-4	68	4.44
Right superior frontal gyrus		24	0	60	5.10	
Left middle frontal gyrus		-48	48	16	5.43	
Left middle frontal gyrus		-28	-12	64	13.08	
Left inferior frontal gyrus		-64	8	16	5.05	
Right inferior frontal gyrus		60	12	32	4.38	
Right inferior frontal gyrus		52	8	12	4.56	
Left cingular gyrus		-8	4	44	11.42	
Right cingular gyrus		4	4	52	7.67	
Left central sulcus		-40	-28	56	14.14	
Left postcentral sulcus		-44	-36	52	10.32	
Right postcentral sulcus		40	-44	52	7.10	
Left superior parietal lobule		-12	-68	56	6.07	
Right superior parietal lobule		16	-68	52	5.07	
Right supramarginal gyrus		64	-32	28	4.92	
Left insula		-36	16	8	4.40	

(continued)

Table 1. Continued.

Task	Anatomical Region	Talairach Coordinates			T Value
Painting	Left superior frontal gyrus	-12	-8	60	8.82
	Right superior frontal gyrus	4	4	56	8.39
	Right middle frontal gyrus	24	0	56	7.32
	Left cingular gyrus	-8	4	44	7.07
	Left precentral sulcus	-32	-12	64	9.56
	Left central sulcus	-40	-28	56	9.40
	Left postcentral sulcus	-36	-44	56	8.25
	Left superior parietal lobule	-16	-76	48	11.37
	Right superior parietal lobule	16	-68	52	11.30
	Right superior parietal lobule	36	-48	56	5.29
	Right IPS horizontal segment	40	-40	60	4.89
	Left precuneus	-8	-60	56	5.18
	Right IPS posterior segment	28	-76	32	4.76
	Left anterior putamen	-24	12	4	5.07
	Right anterior putamen	24	4	4	4.45
	Left thalamus	-12	-20	8	5.27
Attention	Right superior frontal gyrus	4	4	60	3.79
	Left middle frontal gyrus	-36	44	32	4.95
	Left middle frontal gyrus	-28	-8	64	4.37
	Right middle frontal gyrus	24	64	28	4.83
	Right middle frontal gyrus	40	16	36	5.60
	Right inferior frontal gyrus	48	36	0	6.10
	Right postcentral sulcus	44	-40	52	7.02
	Right superior parietal lobule	24	-64	60	6.91
	Left IPS horizontal segment	-36	-60	60	3.35
	Right supramarginal gyrus	56	-44	32	4.08
	Left precuneus	-4	-60	48	7.32
	Right precuneus	8	-64	52	7.27

The table shows the coordinates of the local maxima of significance within the Montreal Neurological Institute (MNI) coordinate system, with t values for the contrast between primary task and control task. IPTO, junction of intraparietal and transverse occipital sulci.

ment of the intraparietal sulcus, and the posterior part of the superior parietal lobule. Finally, an activation was seen in the left insula.

Pointing

Inspection of the activation during the pointing task showed a considerable overlap with the grasping task, including left central sulcus, left precentral and left postcentral activation, bilateral mesial superior frontal gyrus activation at the level of the supplementary motor area, and bilateral anterior cingulate activation. However, important differences with grasping were observed in the parietal lobe. While pointing caused a bilateral activation of the horizontal segment of the intraparietal sulcus, there was little or no anterior supramarginal activity, but there was a clear activation of the posterior part of the superior parietal lobule bilaterally, extending into the left precuneus. Finally, we observed a symmetrical activation of the anterior putamen and a left thalamic activation.

Saccades

The saccades task yielded a distinct network of regions with three components. First, there was a bilateral cluster lying at the intersection of the superior frontal, the middle frontal, and the precentral gyrus, corresponding to the known localization of the frontal eye fields (Corbetta et al., 1998). Second, there was activation in the mesial portion of the posterior superior frontal gyrus, plausibly corresponding with the supplementary eye field area (Grosbras et al., 1999). Third, there was an extended bilateral area of activation in the posterior

parietal region. From front to back, the active areas were the posterior superior parietal lobules and the horizontal and posterior segments of the intraparietal sulcus, extending down to the transverse occipital sulcus. The right putamen, right globus pallidus, and left thalamus were also active.

Attention

The attention task consistently yielded a lower degree of activation than the other tasks. Nevertheless, movements of visual attention activated areas partially similar to those seen in the saccades task. The frontal network showed bilateral activations again lying at the intersection of the superior frontal, the middle frontal, and the precentral gyrus, but with a predominance in the right hemisphere where the activation extended downwards into the precentral sulcus. Bilateral activation was also observed in the lateral prefrontal cortex within the superior frontal sulcus. A small cluster was observed in the right inferior frontal gyrus (BA 45). In the parietal lobe, a bilateral activation was detected in the superior parietal lobule, the precuneus, and the horizontal and superior part of the posterior segment of the IPS, with an anterior extension to the posterior part of the postcentral sulcus in the right hemisphere.

Calculation

Activation was bilateral with a left hemisphere predominance. A large left cluster included the superior frontal gyrus, the precentral sulcus extending into dorsolateral prefrontal cortex, and the inferior prefrontal gyrus (BA 44/45). Similar but smaller activation was observed in

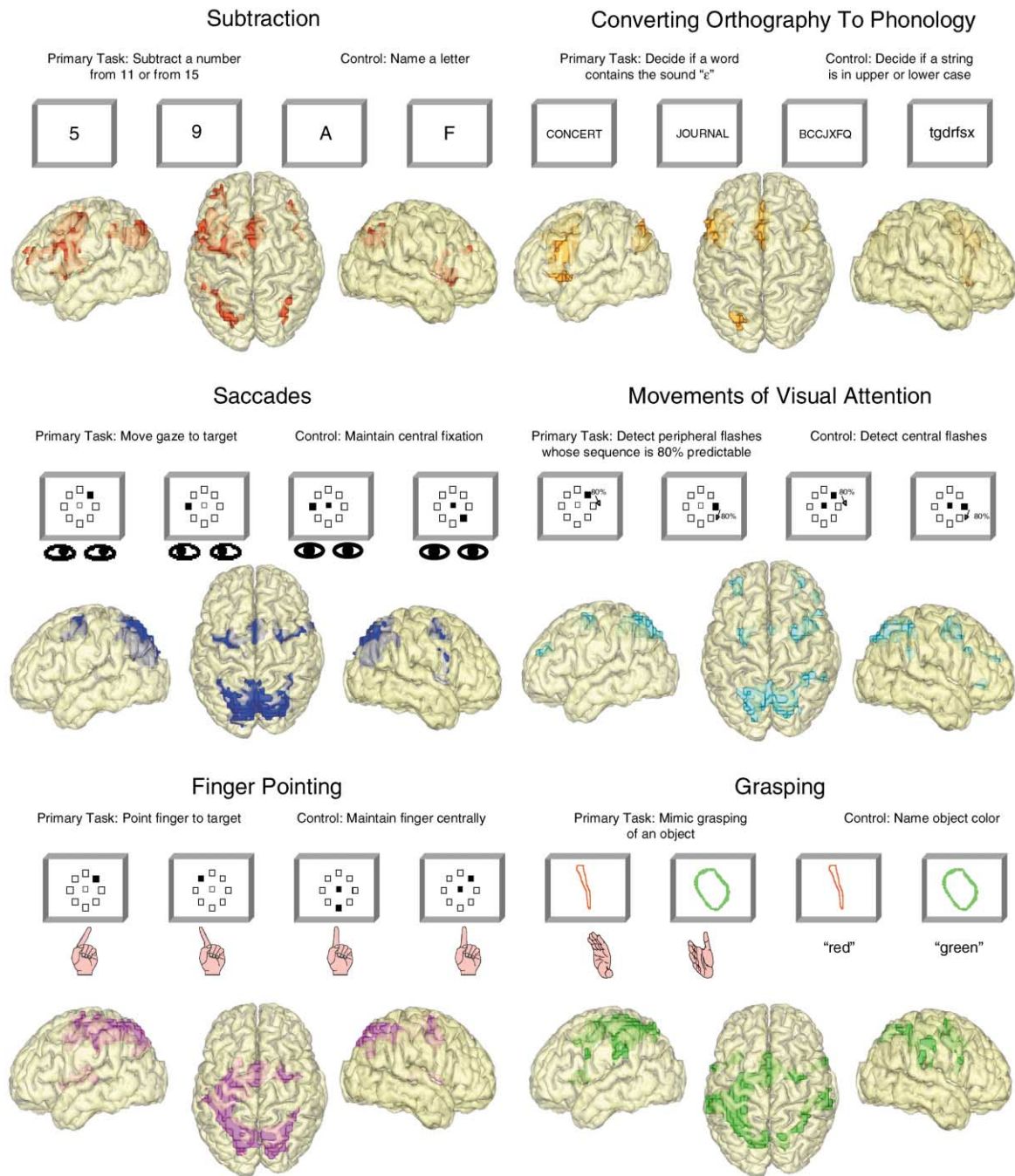


Figure 1. Schematic Depiction of the Six Pairs of Primary and Control Tasks
The corresponding group activations are shown on left, top, and right views of a transparent three-dimensional brain.

the right hemisphere in the superior and inferior frontal gyri. A bilateral activation was detected in the cingulate gyrus. In the parietal region, activation was also predominant in the left hemisphere, where it extended along the intraparietal sulcus from the most superior part of the posterior segment to the postcentral sulcus. In the right hemisphere, only the horizontal segment of the IPS was activated. Finally, activation was observed bilaterally in the anterior putamen, left insula, left putamen, and left thalamus.

Phoneme Detection

This task yielded activation essentially confined to the left hemisphere. A large activation was detected in the left inferior frontal gyrus in the region corresponding to Broca's area (BA 44/45). Prefrontal activation extended to posterior sectors of the left middle and superior frontal gyri, including the precentral gyrus. A mesial activation was also observed bilaterally in the supplementary motor area and anterior cingulate sulcus. In the parietal lobe, only a left cluster was present situated in the angu-

Table 2. Task-Specific Regions

Intersections	Anatomical Regions	Talairach Coordinates			Pairwise Comparisons				
					Ca-Gr	Ca-Po	Ca-Sa	Ca-At	Ca-Lg
Calculation only	Left IPS horizontal segment	-36	-60	36	1.7 10 ⁻⁴	1.1 10 ⁻⁵	4.9 10 ⁻⁴	9.6 10 ⁻⁴	7.8 10 ⁻³
					Gr-Po	Gr-Ca	Gr-Sa	Cr-At	Gr-Lg
Grasping only	Left postcentral sulcus	-28	-44	68	3.7 10 ⁻⁶	6.2 10 ⁻⁶	1.4 10 ⁻³	1.5 10 ⁻⁴	1.4 10 ⁻⁶
	Left postcentral sulcus	-44	-36	40	1.7 10 ⁻⁵	1.8 10 ⁻⁶	1.2 10 ⁻⁴	8.5 10 ⁻⁵	3.6 10 ⁻⁷
	Left postcentral sulcus	-60	-32	36	1.3 10 ⁻⁷	7.1 10 ⁻⁸	6 10 ⁻⁶	4.8 10 ⁻⁷	3.1 10 ⁻⁴
	Left postcentral sulcus	-48	-40	60	3.6 10 ⁻⁴	5.6 10 ⁻⁵	4.4 10 ⁻⁵	1.1 10 ⁻⁴	1.5 10 ⁻⁶
	Right postcentral sulcus	36	-44	60	7.2 10 ⁻³	1.1 10 ⁻⁴	1.1 10 ⁻⁴	7.1 10 ⁻³	3.1 10 ⁻⁵
	Right postcentral sulcus	64	-32	24	3.2 10 ⁻⁴	3.1 10 ⁻⁴	1.1 10 ⁻³	6.3 10 ⁻⁴	3.1 10 ⁻⁵
Saccades only	Left SPL posterior segment	-8	-88	36	3.1 10 ⁻³	5 10 ⁻⁴	7.5 10 ⁻⁴	5.1 10 ⁻⁵	8 10 ⁻⁵
					Left IPTO	-24	-84	24	2.8 10 ⁻³
	Right IPS posterior segment	28	-64	48	3.9 10 ⁻⁵	1.4 10 ⁻⁴	2.6 10 ⁻³	10 ⁻⁴	9.9 10 ⁻⁶
	Right SPL posterior segment	8	-84	36	1.8 10 ⁻⁵	3.7 10 ⁻⁴	6 10 ⁻³	5.1 10 ⁻¹³	1.9 10 ⁻⁴
	Right IPTO	28	-80	24	6.8 10 ⁻⁴	1.8 10 ⁻³	2.4 10 ⁻³	1.1 10 ⁻⁴	6.3 10 ⁻³
					At-Gr	At-Po	At-Ca	At-Sa	At-Lg
Attention only	Left precuneus	-4	-52	52	6.6 10 ⁻⁶	9.8 10 ⁻³	2.9 10 ⁻⁵	2.4 10 ⁻³	1.8 10 ⁻⁴

The reported regions were significantly active ($p < 0.01$) during the indicated task, and not during the other five tasks. The columns at right show the outcome of all the relevant pairwise comparisons (Gr, grasping; Po, pointing; Sa, saccades; At, attention; Ca, calculation; and Lg, language). The p value indicates the uncorrected voxel-wise significance level at the local maximum closest to the given coordinates. IPS, intraparietal sulcus; SPL, superior parietal lobule.

lar gyrus and in the horizontal segment of the intraparietal sulcus.

Task-Specific Regions

Grasping Only

Two clusters of voxels were activated only in grasping and significantly more during grasping than during any other task. They occupied symmetrical locations in the left and right anterior supramarginal/postcentral regions.

Pointing Only

No parietal region passed all the criteria for a selective response during pointing only.

Saccades Only

Within the parietal lobe, a large posterior cluster was observed bilaterally during saccades only. As shown in Figure 2, this region included bilateral areas of the superior parietal lobule as well as the posterior segment of the intraparietal sulcus extending down to the intersection between the intraparietal sulcus and the transverse occipital sulcus (area IPTO [Wojciulik and Kanwisher, 1999]).

Attention Only

A cluster of voxels situated in the left precuneus was activated during the attention task only. A similar cluster was also observed at the symmetrical location in the right precuneus (coordinates 12, -60, 44). However, its activation was greater during attention than during the calculation, language, or grasping tasks, but not the saccades or pointing tasks.

Calculation Only

Activation induced by calculation only was present in the horizontal segment of the left intraparietal sulcus. Another cluster was observed during calculation and no other task at the symmetrical location in the right hemisphere (coordinates 40, -56, 52). However, it failed to pass all criteria for selectivity: activation was significantly greater for calculation relative to pointing and

language, but not relative to grasping, saccades, and attention.

Language Only

No parietal region passed all the criteria for a selective response during the phoneme detection task only.

Task Intersections

Grasping and Pointing

A large cluster of activation selective for grasping and pointing was observed in the left anterior IPS, extending into the superior parietal lobule and the postcentral sulcus, with a posterior extension into the horizontal segment of the IPS and an anterior extension into the central sulcus. This activation was located posterior and dorsal to the bilateral activation specific to grasping only and immediately dorsal to the activation observed during calculation only.

Four Visuospatial Tasks

Two large clusters occupying symmetrical locations in the left and right superior parietal lobules, dorsal to the posterior horizontal segment of the IPS, were selectively activated during the four visuospatial tasks (grasping, pointing, saccades, and attention).

Calculation, Language, and Saccades

An area of overlap between the calculation, language, and saccades tasks was detected in the left posterior segment of the IPS beneath the left angular gyrus. A small cluster of activation common to the calculation and language tasks, but absent during the other four tasks, was also observed just next to this activation (coordinates -28, -68, 36). However, this region failed to show significantly greater activation during either the language or the calculation task than during the saccade task.

The observation of an intersection between calculation, language, and saccades was unexpected. We reasoned that intersubject averaging and smoothing could have caused the intense saccade-related activations to

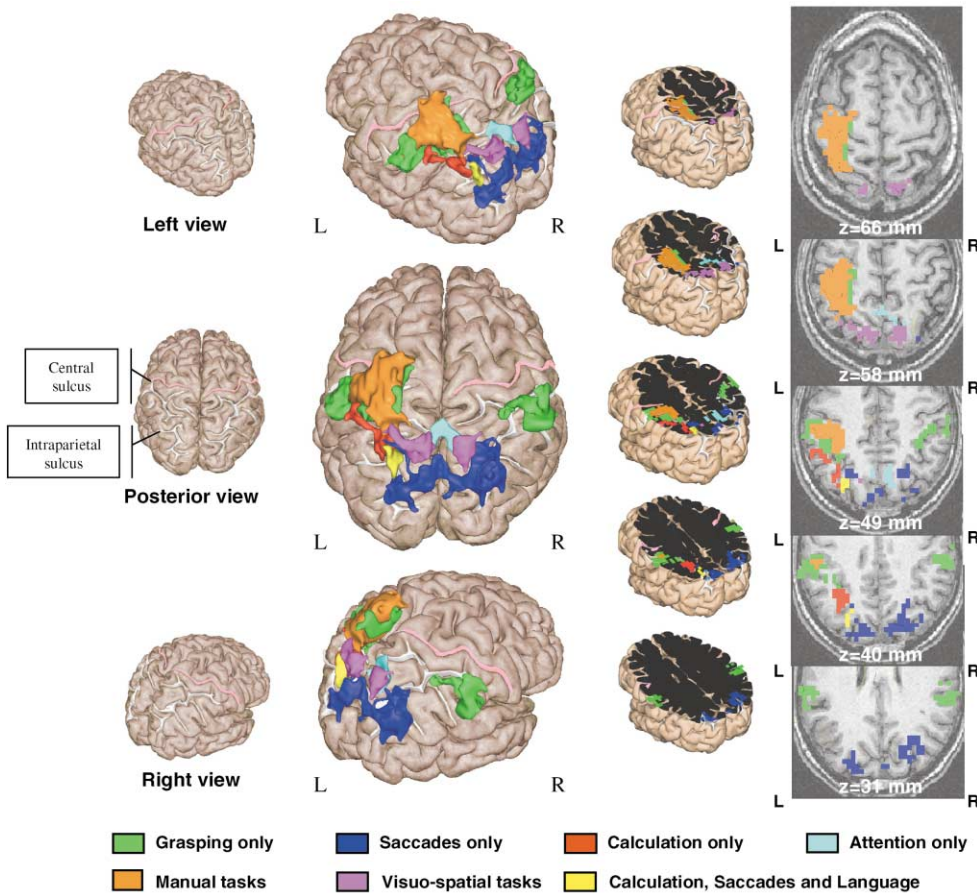


Figure 2. Localization of Task-Specific and Task Intersection Activations in the Group Analysis

Top, three-dimensional view on a transparent brain as seen from a superior posterior viewpoint (for reference, a small anatomical image is shown in the same orientation, with the principal sulcus in pink and the IPS in gray). Bottom, axial slices in MNI space.

artificially spread into language and calculation-related areas. Single subject analyses clarified this point. All subjects showed activation in the left IPS underneath the angular gyrus in the conjunction of calculation and language. Comparison of this activation to the saccade activation at the same threshold revealed a clear dissociation. The calculation and language activations were left lateralized and occupied a lateral position within the IPS, while the saccade activations were bilateral and often occupied a more mesial and dorsal location in the IPS, extending into the SPL (Figure 3). In five out of ten subjects, there was no overlap, and the peak of activation during calculation and language showed no activation during saccades. In four out of ten subjects, there was marginal overlap, since calculation and language activated voxels on the fringe of the main activation for saccades. In only one subject did the calculation and language activation fall strictly within the saccade activation. Examination of peak coordinates confirmed that the activation during calculation and language was variable across individuals, especially in the z direction (mean \pm 1 SD, -31 ± 5 , -70 ± 9 , $z = 43 \pm 12$). We conclude that the area jointly activated by calculation and language was reproducible and dissociable from

the saccade-related activation in single subject data but that this distinction became smeared in the group analysis due to interindividual variability.

Other Intersections Tested

Parietal activation common to the attention and saccades tasks, but not the other tasks, was present in the medial precuneus (coordinates -4 , -56 , 60). This region passed seven out of the eight pairwise tests for greater activation during either saccades or attention relative to any of the other four tasks. However, it failed short of significance in the test for greater activation during attention than during pointing (voxelwise, $p = 10^{-2}$; corrected clusterwise, $p = 0.09$).

Finally, in the parietal lobe, there were no areas specific to calculation and saccades alone; to calculation, saccades, and attention; or to calculation and the manual tasks of grasping and/or pointing. No parietal area was jointly activated by all six tasks.

Discussion

fMRI revealed an orderly organization of activations in the parietal lobe. Because of its focus on calculation and language, our experiment focused on the left pari-

Table 3. Tact Intersections

Intersections	Anatomical Regions	Talairach Coordinates																
Manual tasks only (grasping and pointing)	Left postcentral gyrus	-40	-28	56	Gr-Ca	1.2 10 ⁻⁶	Gr-Sa	6.5 10 ⁻⁸	Gr-Lg	1.4 10 ⁻⁷	Po-Ca	1.2 10 ⁻⁶	Po-Sa	8.6 10 ⁻⁷	Po-At	1.6 10 ⁻⁶	Po-Lg	2.3 10 ⁻⁶
	Left IPS horizontal segment	-36	-44	56	Gr-Ca	5.6 10 ⁻⁵	Gr-Sa	5.1 10 ⁻⁶	Gr-Lg	1.5 10 ⁻⁶	Po-Ca	4.8 10 ⁻⁴	Po-Sa	3.3 10 ⁻⁶	Po-At	1.2 10 ⁻⁴	Po-Lg	7.4 10 ⁻⁶
	Left postcentral sulcus	-32	-44	64	Gr-Ca	6.2 10 ⁻⁶	Gr-Sa	5.1 10 ⁻⁶	Gr-Lg	1.5 10 ⁻⁶	Po-Ca	4.8 10 ⁻⁴	Po-Sa	3.3 10 ⁻⁶	Po-At	1.2 10 ⁻⁴	Po-Lg	7.4 10 ⁻⁶
Visuospatial tasks (grasping, pointing, saccades, saccades and attention)	Left SPL anterior segment	-12	-68	52	Gr-Ca	1.3 10 ⁻⁵	Gr-Sa	2 10 ⁻⁴	Gr-Lg	1.6 10 ⁻⁵	Po-Ca	2 10 ⁻⁴	Po-Sa	1.5 10 ⁻⁵	Po-At	9 10 ⁻³	Po-Lg	2.1 10 ⁻⁶
	Right SPL anterior segment	16	-68	52	Gr-Ca	5.9 10 ⁻⁴	Gr-Sa	6.4 10 ⁻⁵	Gr-Lg	5.3 10 ⁻⁷	Po-Ca	2.5 10 ⁻⁴	Po-Sa	1.2 10 ⁻⁶	Po-At	6 10 ⁻³	Po-Lg	2.9 10 ⁻⁵
Calculation, saccades, and language	Left IPS posterior segment	-32	-72	44	Ca-Gr	2 10 ⁻⁵	Ca-Po	6.9 10 ⁻³	Sa-Gr	2.1 10 ⁻⁵	Sa-Po	3.6 10 ⁻⁴	Sa-At	1.3 10 ⁻⁴	Lg-Gr	6.7 10 ⁻⁵	Lg-Po	2.1 10 ⁻³

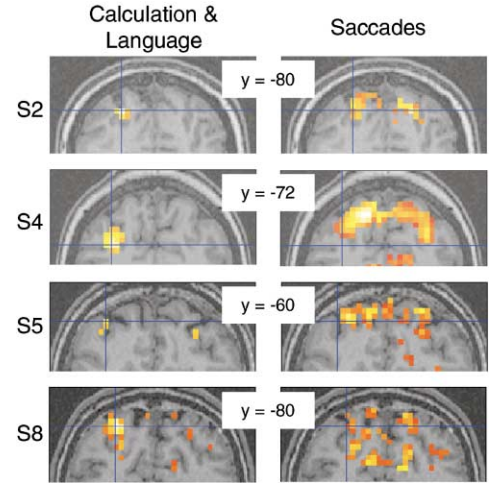


Figure 3. Relative Locations of the Saccade-Related Activation and of the Conjunction of Calculation and Language in the Left Posterior IPS in Four Representative Subjects

etal lobe, and we asked subjects to perform the manual tasks with their right hand only. Nevertheless, several elements of the observed “parietal map,” including the regions involved in grasping and in the four visuospatial tasks, were symmetrically organized in the two hemispheres. This suggests their involvement in higher level visuospatial representations rather than mere contralateral hand movement.

We focused on a group analysis averaging over ten subjects. However, analyses of the individual data indicate that the major circuits associated with each task were present in all subjects with a same systematic topographical organization of the major task intersections. Obviously, our ability to delineate areas of activation common to multiple tasks is limited by the spatial resolution of the images (4 × 4 × 4 mm), their smoothness (about 11 × 11 × 11 mm in the final normalized images), and the intersubject averaging. Therefore, some of the areas identified as common to several tasks may in fact comprise multiple, interlaced, specialized subsystems whose size cannot be resolved at present. Artifactual areas of intersection might also have been created by spatial smoothing at the boundary separating two specialized regions. Further experiments with single subjects and a higher spatial resolution are needed to clarify those points.

Possible Homologies with Monkey Parietal Areas

The systematic, functional organization that we observed in human subjects during visuomotor tasks bears significant relation to the organization of the monkey parietal lobe (Rizzolatti et al., 1998). Because our tasks were not designed for direct comparability with electrophysiological studies, any identification of homologies must remain tentative. Nevertheless, human homologs of the monkey areas AIP, MIP, V6a, and LIP are suggested.

Grasping and Areas AIP and F5

Activation specific to the grasping task, and not observed during pointing, was found bilaterally in the ante-

rior part of the inferior parietal lobule within the banks of the inferior postcentral sulcus, which constitutes the anterior and inferior extension of the IPS. Similar activation was observed during previous studies of actual or imagined grasping (Binkofski et al., 1998; Decety et al., 1994; Faillenot et al., 1997; Grafton et al., 1996), as well as during observation of grasping movements (Buccino et al., 2001). Grafton et al. (1996) also observed anterior inferior parietal activation during grasping but interpreted it as an engagement of the secondary somatosensory area (SII). This interpretation can be rejected in the present case because our task did not involve the actual touch of an object. Furthermore, area SII is consistently localized in the upper bank of the Sylvian fissure immediately posterior to the central sulcus (Disbrow et al., 2000) and thus inferior to the activation observed in the present study.

Our grasping-specific area appears as a plausible analog of monkey area AIP (anterior intraparietal), a region involved in the visually guided shaping of the hand (Murata et al., 2000; Sakata et al., 1995). Its tentative coordinates in humans, rounded to the nearest centimeter, would then be $\pm 60, -30, 40$. In humans, the lower extent of the postcentral sulcus, within which the grasping-specific activation is found, lies in continuity with the intraparietal sulcus and hence constitutes a plausible homolog of the anterior intraparietal sulcus in monkeys. AIP neurons are active during grasping/manipulation movements, presentation of visual objects, or both. Gallesse et al. (1994) have shown that AIP inactivation results in a deficit of hand shaping for grasping objects, with no deficit in the reaching component of the movement. This is highly similar to human subjects in whom anterior intraparietal lesions result in selective deficits of the coordination of finger movements required for grasping (Binkofski et al., 1998).

The main frontal target of area AIP is the ventral premotor area F5 (Luppino et al., 1999), which contains mirror neurons activated during both action execution and action recognition (Rizzolatti et al., 1998). We also observed a bilateral inferior prefrontal activation in Brodmann's area 44, which is thought to be the human homolog of area F5 (Iacoboni et al., 1999; Rizzolatti et al., 1998). Together, F5 and AIP may constitute a circuit for the visual guidance of hand movements, which is present in both humans and monkeys.

Goal-Directed Hand Movements and Areas MIP and PE

We also observed hand movement-related activation in a left-lateralized cluster of voxels ranging from the central sulcus to the postcentral sulcus, the superior parietal lobule, and the horizontal segment of the IPS contralateral to the moving hand. It clearly encompassed the primary motor and somatosensory hand areas. However, its posterior extension into the left middle IPS requires more discussion. This area was strongly activated during both grasping and pointing movements but totally inactive during eye or attention movements, calculation, and phoneme detection. A similar, though smaller, focus was observed in the right middle IPS.

Given that the pointing and saccade tasks involved similar stimuli, the dissociation between them suggests

that this area is specialized for visually guided hand movements (Kawashima et al., 1996). It may encompass the human homolog of the monkey area MIP (medial intraparietal; tentative coordinates in humans, $-40, -40, 60$). MIP neurons code for peripersonal space in terms of its accessibility by the arm (Eskandar and Assad, 1999) or by a tool (Iriki et al., 1996). They are selectively modulated by the direction of an upcoming hand or arm movement even when the direction is distinct from the direction of visual motion (Eskandar and Assad, 1999). Through its connections with areas V6A, LIP, and the premotor cortex, area MIP plays a critical role in spatially directed hand movements (Colby, 1998). This function was clearly required during the pointing task but presumably also during the grasping task since it required programming finger movements appropriate to the location and orientation of visually presented objects.

Our paradigm was not designed to separate area MIP from other regions that also contribute to motor action. Indeed, we also observed activation of the superior parietal lobule during both grasping and pointing. In monkeys, the convexity of the superior parietal lobule is formed by area PE, which is thought to be involved in the elaboration of proprioceptive information (Rizzolatti et al., 1998). Some PE neurons are activated by passive joint rotation or active limb movements, while others combine tactile and joint information (Mountcastle et al., 1975). Altogether, area PE may be involved in the representation of the body in space. Such a representation was clearly essential in the grasping and pointing tasks where subjects attended to their hand and finger orientation information in darkness.

Saccades, Attention, and Areas LIP, 7a, V6, V6a, and PEc

The saccades task and the attention task both lead to the activation of the bilateral dorsal parietal lobe. Many of the active areas were common to attention and saccades. The area of intersection included the bilateral dorsal superior parietal lobule, which was also activated during grasping and pointing, and a mesial region in the precuneus, which also tended to be activated by the pointing task. Attention and saccades also jointly activated the bilateral frontal eye fields and supplementary eye fields. This replicates earlier results (Corbetta et al., 1998; Nobre et al., 2000) and supports the hypothesis of a tight linkage between attention and eye movements (Rizzolatti et al., 1987). A new outcome of the present study, however, is that a major component of this circuit, located in the mesial and dorsal bank of the posterior intraparietal sulcus and neighboring superior parietal cortex, is also very strongly activated during grasping and pointing tasks in the absence of overt eye movements. Wojculik and Kanwisher (1999) also found this area to be activated during three different forms of attention: peripheral attention shifting, sustained attention to parafoveal locations, and temporal attention to feature conjunctions. They suggested that its function was not the mere shifting of gaze and attention across locations, but rather, the suppression of task-irrelevant distractors. It is unclear, however, why the grasping task would require suppression since no distractors were pre-

sented. The present data merely allow us to suggest that this region plays a general role in the selection of objects for pending actions, whether the actions are purely mental or involve actual object-directed hand or eye movements.

We also found some dissociations between the saccades and attention networks. Saccades yielded greater activation in the bilateral postero-mesial intraparietal sulcus, close to its intersection with the transverse occipital sulcus (region IPTO), in the bilateral posterior superior parietal lobule, and in the right posterior IPS. Previous studies have observed IPTO activation in humans during attention tasks without any overt saccades (Corbetta et al., 1998) or indeed without even any form of movement planning (Wojciulik and Kanwisher, 1999). Thus, it is unclear why our attention task, as well as another study of covert attention orienting (Gitelman et al., 1999), failed to activate this area. A lack of statistical sensitivity cannot be excluded. Because only two short fMRI sequences were available for each task, our images may underestimate the attention network.

Conversely, greater activation for attention than for saccades was observed in the precuneus, thus revealing a double dissociation. Some, but not all, imaging studies of covert attention report precuneus activation during visual attentional tasks (Corbetta et al., 1998; Gitelman et al., 1999; Nobre et al., 2000). The origin of this discrepancy is not understood. Note that the attention task used 80% predictable targets, while the saccade task used unpredictable targets. The active anticipation of an upcoming target may lead to the activation of visual imagery processes with which the precuneus has been tentatively related (Fletcher et al., 1996). Active anticipation may also explain the bilateral anterior dorsolateral prefrontal activation, which, like the precuneus activation, was observed solely during the attention task (Figure 1).

In terms of homologies to the monkey brain, the human areas activated during saccades, attention, or both are likely to contain homologs of the monkey areas 7a (also called PG), LIP, V6, V6a, and PEc. All of these areas contain neurons that encode the location of visual stimuli and modulate their activity as a function of whether the animal intends to make an eye movement toward them (Colby et al., 1996; Rizzolatti et al., 1998; Snyder et al., 1998). The area jointly activated by all four visuospatial tasks (saccades, attention, pointing, and grasping) might correspond to area V6a (tentative coordinates in humans: ± 15 , -70 , 50). Recordings in V6a and the neighboring area PEc reveal a joint selectivity for movements of the hand and eye at the single neuron level (Battaglia-Mayer et al., 2001). Furthermore, the monkey V6a is located on the just posterior and mesial to area MIP, which fits well with our observed localization in the superior parietal lobule just dorsal to the horizontal segment of the IPS. The precuneus activation during attention might then relate to the monkey area PEc (tentative coordinates in humans: 0 , -50 , 50).

Finally, for the posterior saccade-related activations, two identifications have been proposed. The medial parieto-occipital sulcus has been proposed as the human homolog of the monkey V6 complex (Portin and Hari, 1999), a high-level visual region (Galletti et al., 1999) where neural activity is strongly modulated by eye posi-

tion (Galletti et al., 1995) (tentative coordinates in humans: ± 25 , -80 , 20). The human posterior intraparietal region active during saccades has been proposed as a "posterior eye field" homologous to area LIP (lateral intraparietal) (Muri et al., 1996). We observed bilateral activation during saccades in the posterior IPS, although the left activation was partially masked by the language and calculation activation in the group's results, as noted above. Our tentative coordinates for this area (± 30 , -60 , 50) fit nicely with those recently obtained using the method of retinotopic mapping (Serenio et al., 2001). As noted by Van Essen et al. (2001), and further discussed below, this localization implies a considerable posterior displacement of area LIP in humans relative to monkeys.

Calculation and Language-Related Activations in the Human Inferior Parietal Lobule

The main goal of our experiment was to localize calculation and language-related activations in the human parietal lobe and to examine their relative location and overlap with other visuospatial activations. During a subtraction task, activation was observed bilaterally in the lateral bank of the intraparietal sulcus, replicating earlier work (Chochon et al., 1999; Dehaene et al., 1999; Lee, 2000; Stanescu-Cosson et al., 2000; Zago et al., 2001). This activation did not overlap with those observed during grasping, pointing, saccades, or attention movements. However, examination of the overlap with the phoneme detection task revealed a separation into two regions. The middle portion of the IPS corresponding to its horizontal segment underneath the supramarginal gyrus was activated bilaterally, though with greater intensity in the left hemisphere, solely during the subtraction task. However, a more posterior and strictly left-lateralized region of IPS underneath the angular gyrus was activated jointly by calculation and phoneme detection.

The presence of two neighboring regions for calculation within the left IPS, only one of which is shared with phonological processing, fits with the theoretical hypothesis that number processing relies on the coordination of two different representations of numbers: a nonverbal quantity code involving the bilateral intraparietal sulci and a verbal code involving classical language areas including the left angular gyrus (Dehaene and Cohen, 1995, 1997; Dehaene et al., 1998). Activation of the left angular gyrus was previously observed during operations that require access to a rote verbal memory of arithmetic facts, such as single digit addition or multiplication (Chochon et al., 1999; Lee, 2000; Zago et al., 2001). In particular, its coordinates match with those of the angular gyrus activation previously observed during exact arithmetic fact retrieval relative to calculation approximation (Dehaene et al., 1999; Stanescu-Cosson et al., 2000). During fact retrieval, subjects are thought to basically "read out" the result of visually presented problems from their verbal memory. Indeed, overlapping activations were observed during rote calculation and during phoneme detection, not only in the left angular gyrus, but also in the left inferior frontal gyrus extending toward the anterior insula, the left premotor cortex, and the left supplementary motor area. Those areas consti-

tute a classical circuit for reading (Fiez and Petersen, 1998; Price, 1998). The precise contribution of the left angular gyrus within this language circuit remains to be specified. According to Hickok and Poeppel (2000), the inferior parietal lobule serves as an auditory-motor interface in language processing, connecting the left temporal areas for phonological speech analysis to frontal areas for articulatory speech production. Such a function would be in line with the general role of the parietal lobe in sensorimotor conversion operations.

Although some subtraction problems may be stored in verbal memory, many are not learned by rote and therefore require novel quantity manipulations. Quantity manipulation can be plausibly related to the calculation-specific bilateral activation of the middle intraparietal region. This region was previously found to show greater activation during approximation than during exact calculation (Dehaene et al., 1999; Stanescu-Cosson et al., 2000) and during subtraction more than during multiplication (Chochon et al., 1999; Lee, 2000). Bilateral intraparietal activation has also been observed during simpler quantity processing tasks that do not involve calculation, such as deciding which of two Arabic numerals is the larger (Chochon et al., 1999; Pesenti et al., 2000; Pinel et al., 2001). Using single event fMRI in a parametric design, Pinel et al. (2001) recently demonstrated that the activation of this region during number comparison was independent of whether the numbers were presented as words or as Arabic digits but was inversely proportional to the semantic distance between the numbers to be compared. For such reasons, this region is thought to encode the proximity relations among numerical quantities in a nonverbal format akin to a mental "number line" (Dehaene et al., 1998). The insertion of this region amid other visuospatial maps fits with this hypothesis of an internal mental space for numbers. During number comparison and approximation tasks, the intraparietal region coactivates together with the bilateral superior parietal lobule and precuneus (Dehaene et al., 1999; Pinel et al., 2001; Stanescu-Cosson et al., 2000) at sites coincident with those observed for saccades, attention, and the four visuospatial tasks. This suggests that these number processing tasks call for generic processes of attention orientation and spatial manipulation that operate upon a "spatial map" of numerical quantities in the middle IPS.

Concluding Remarks on Monkey-Human Homologies

Our study identified two lateral intraparietal areas associated with functions particularly developed in the human species: calculation and phoneme detection. Those areas were surrounded by visuospatial areas plausibly homologous to the monkey areas AIP, MIP, V6A, and LIP. This organization of areas fits well with the cytoarchitectonic parcellation of the human parietal lobe proposed by Eidelberg and Galaburda (1984). Both studies suggest a considerable expansion and differentiation of the inferior parietal lobule in humans compared with monkeys. In particular, Eidelberg and Galaburda (1984) identify a left-lateralized field PG in the human angular gyrus, which may correspond to the strictly left-lateralized region that we found active during phoneme detection.

Recently, Van Essen et al. (2001) attempted to establish a correspondence between macaque and human brains by matching computerized surface-based atlases across species. In the posterior and superior parietal lobule, their warped map fits well with our tentative localization for areas V6a/PEc (PO in their scheme), MIP, and PE (MDP in their scheme). However, they note that warping, even though it implies a 20-fold expansion of the parietal surface, does not provide a satisfactory account of the human IPS and inferior parietal lobule. In particular, the warping algorithm projects monkey area LIP onto the horizontal segment of the IPS, at a region where no saccadic activation is observed in humans (Corbetta et al., 1998). Saccade-related activity is found more posteriorly in the human IPS than predicted by mere warping. Our data suggest that, in the course of hominid evolution, areas AIP and LIP have become increasingly separated in cortical space as a consequence of the expansion of the inferior parietal lobule where activations related to uniquely human activities of calculation and language are observed. Because some animals do exhibit rudimentary abilities for calculation (Dehaene et al., 1998), our results suggest that an evolutionary precursor of number processing in primates, if it exists, might be found in the anterior part of area LIP, the dorsal sectors of areas 7a (PF), 7b (PG), or the intermediate area PFG.

Experimental Procedures

Subjects

Ten neurologically normal right-handed volunteers (7 females; mean age 25, range 22–34) gave informed consent to participate in the study, which was approved by the regional ethical committee. Four additional subjects were tested and rejected. Two had excessive movement artifacts. Two others exceeded our criteria of mean response time lower than two seconds and mean error rate lower than 20%: one subject failed in the calculation test and the other in the language test.

Procedure

Cerebral activation was studied in each six conditions: subtraction, grasping, pointing, saccades, visuospatial attention, and phoneme detection. Each of these primary tasks was compared to a control task matched for stimulus characteristics. During an fMRI scanning sequence, 6 blocks of 13 trials each (26 s), preceded by a 4 s instruction period were presented, with an alternation of primary task and control task blocks. Each subject performed two such sequences for each of the six tasks, resulting in 12 fMRI sequences. Prior to scanning, subjects also participated in a training session with a single run of each task.

Stimuli were presented with an active matrix video projector on a dark background at the rate of 2 s per trial, synchronized with the acquisition of an fMRI volume, using *expe6* software (Pallier et al., 1997). All stimuli were presented for 150 ms to prevent undesired saccades. Subjects were instructed to avoid eye movement during all tasks except the saccades task. No arm movement was allowed except during grasping and pointing tasks. The adequacy of eye and hand movements was assessed visually during the training period.

Saccades Task

This task isolated the circuit for visually guided eye movements (Muri et al., 1996). The visual display consisted of eight small red boxes regularly arranged on a circle at 6° eccentricity from a similar box centered on screen (see Figure 1). In the primary saccade task, on each trial, a filled white square appeared within a randomly chosen box for 150 ms and was replaced by a fixation cross centered in the box. Subjects had to move their eyes toward this box and

fixate it for 2000 ms until the next trial appeared. In the control fixation task, subjects were asked to maintain fixation on a fixation cross that stayed within the central box while distracting white squares appeared randomly in the periphery.

Pointing Task

This task isolated the circuit for visually guided finger-pointing movements. The stimulus was similar to the saccade task except that the fixation cross remained in the central box throughout. In the primary pointing task, subjects were asked to point their right index finger in the direction of the box where a filled white square appeared while maintaining their gaze on the central box. In the control fixation task, subjects kept their finger pointed at the central box, neglecting randomly appearing peripheral distractors. Note that our subjects were asked to move only the index finger and to keep their hand, wrist, and arm still. This "pointing" task differs from the classical "reaching" task where subjects extend their arm to touch a target with the finger. Nevertheless, our activations during pointing were similar to published reports using reaching (Grafton et al., 1996; Kawashima et al., 1996).

Attention Task

This task was inspired by Corbetta et al. (1998) and measured covert shifts of visual attention. Throughout the experiment, subjects were asked to detect, with a right hand key press, the sudden appearance of an asterisk within the same boxes as in the above saccades and pointing tasks. The onset of the stimuli was randomized relative to trial onset (flat distribution, 0–400 ms). The primary attention task was designed to induce shifts of attention to peripheral locations within a visual field. Targets appeared at predictable locations on the peripheral circle, in a clockwise order, with an 80% probability. On the remaining 20% of trials, another unpredictable location was probed. Subjects were informed of the partial predictability of the stimuli and were instructed to shift attention, in advance of each trial, to the most probable location of the upcoming item. The efficacy of these attentional instructions was monitored by comparing the reaction times (RTs) with predictable and unpredictable trials. A significant difference was found (303 versus 383 ms; $t(9\text{ df}) = 4.83$, $p < 0.001$). The control task was intended to prevent orienting of attention to peripheral locations by engaging subjects' attention in the center. Subjects responded to asterisks presented in the central fixation box, while peripheral asterisks were also flashed simultaneously at random peripheral locations. Response times were fast (295 ms) and no different from those observed on predictable peripheral trials ($t(9\text{ df}) = 1.07$).

Subjects were instructed to refrain from moving their eyes throughout the experiment. During training, subjects made at most one saccade during the entire experiment (mean = 0.26% saccades per trial).

Grasping Task

This task identified cortical areas for visually guided hand-grasping movements. To simplify stimulus presentation in the fMRI scanner, we used a pantomime task without actual object grasping. Although there are important differences between pantomimed and actual grasping (Goodale et al., 1994), both require using a visuomotor transformation, presumably implemented in parietal circuitry, to shape and orient the hand in relation to a visual stimulus. Indeed, pantomimed grasping lead to parietal activations comparable to those of earlier studies using actual grasping (Binkofski et al., 1998; Faillenot et al., 1997; Grafton et al., 1996). The stimuli were eight different outline shapes appearing in ten different orientations and in four different colors (green, blue, red, or yellow). In the primary grasping task, subjects had to move their right hand and wrist as fast and precisely as possible in order to mimic grasping of the object. In the control task, subjects kept their hand still and mentally named the color of the objects.

Phoneme Detection Task

This task identified the cortical circuitry of word reading (Fiez and Petersen, 1998), with particularly emphasis on the possible contribution of parietal cortex to the conversion from orthography to phonology (Price, 1998). In the primary phoneme detection task, the stimuli

were French concrete words, five to eight letters long, with frequency higher than one per million. Eighty percent of the words contained the sound "e" or "é." Subjects were instructed to mentally sound out the words and to detect stimuli containing the sound "e" or "é" by depressing a right hand button as quickly as possible. Each word was seen only once during the entire experiment. In the control case-detection task, the stimuli were letter strings matched to the words in number of letters. Eighty percent of these strings were in upper case. Subjects were instructed to detect uppercase stimuli by pressing a right hand button. Subjects were significantly slower in phoneme detection than in case detection (644 versus 481 ms; $t(9\text{ df}) = 6.70$, $p < 0.001$), but the error rates did not differ (7.0% versus 5.2%; $t(9\text{ df}) = 1.75$, $p > 0.10$).

Calculation Task

This task identified cortical areas associated with simple mental calculation (Chochon et al., 1999). In the primary calculation task, stimuli were Arabic digits from 2 to 9. Subjects were instructed to subtract each number from a fixed reference (11 in the first run, 15 in the second) and to mentally name the result. In the control naming task, stimuli were uppercase letters between B and J, excluding letter I. Subjects were asked to mentally name each letter. Both response times and error rates were significantly higher in the calculation task than in the control task (RTs, 881 versus 553 ms; $t(9\text{ df}) = 13.2$, $p < 0.001$; errors, 5.0 versus 0%; $t(9\text{ df}) = 2.65$, $p < 0.03$).

Imaging Parameters

Functional MR images were acquired on a Siemens Signa 1.5T whole-body scanner. Sequence parameters were Gradient-echo EPI, TE = 60 ms, TR = 2 s, flip angle = 90°, slice thickness = 3.8 mm, interslice gap = 0, image matrix = 64 × 64, FOV = 192 × 256 mm, and functional voxel size = 3.75 × 3.75 × 3.8 mm³. 18 axial slices were acquired covering the parietal lobe and the majority of the prefrontal cortex, excluding the orbitofrontal sector. Each task sequence consisted of 97 18-slice scans, the first 4 of which were not analyzed. Three-dimensional high-resolution anatomical images were also acquired (TE = 2.2 ms, TR = 10 ms, flip angle = 10°, inversion time (TI) = 600 ms, matrix = 256 × 192 mm, FOV = 220 × 165 mm, 128 sagittal slices, and slice thickness = 1.5 or 1.2 mm).

Statistical Analyses

The data from each individual subject was processed with Statistical Parameter Mapping software (SPM99). Following motion correction, normalization to the Montreal Neurological Institute (MNI) template, and minimal spatial smoothing (5 mm), the activation in each session was modeled using a linear combination of two functions obtained by convolving the known temporal profile of the primary and control blocks with the standard hemodynamic function of SPM. Single subject data were analyzed with simple contrasts for greater activation during each primary task than during its control and with all 30 pairwise contrasts for greater activation in one task than in another (voxelwise, $p < 0.001$; cluster level, $p < 0.05$, corrected).

Group analyses were performed with random effects analyses. We first examined, for each of the six primary tasks relative to their respective controls, the entire set of areas showing a significant activation (voxelwise, $p < 0.01$; cluster level, $p < 0.05$, corrected). We then performed random effects analyses of all the 30 pairwise comparisons between two tasks. For those pairwise comparisons, the search was confined to voxels belonging to the parietal lobe and which showed activation in at least one of the six tasks of interest. The voxelwise threshold was again set at $p < 0.01$, and the cluster extent threshold was set to $p < 0.05$, corrected for multiple comparisons across the parietal volume (using the small volume correction option of SPM99; minimal cluster size, 9 voxels). A complete table of those results is available from the authors. Here, a region is reported only if (1) all of its voxels passed a threshold for significance of $p < 0.01$ for the tasks of interest; (2) all of its voxels failed to pass this threshold for the remaining tasks; (3) all of the appropriate pairwise comparisons, as described above, identified a significant region encompassing this location; and (4) the volume of the region was at least 26 voxels.

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