

Neural correlates of mental transformations of the body-in-space

(parietal cortex/body knowledge/positron emission tomography)

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ABSTRACT Regional cerebral blood flow was measured with positron emission tomography in human subjects during the performance of a task requiring mental rotation of their hand and a perceptually equivalent control task that did not require such a process. Comparison of the distribution of cerebral activity between these conditions demonstrated significant blood flow increases in the superior parietal cortex, the intraparietal sulcus, and the adjacent rostralmost part of the inferior parietal lobule. These findings demonstrated that, in the human brain, there is a specific system of parietal areas that are involved in mental transformations of the body-in-space.

Patients with lesions of the parietal region of the brain exhibit various disturbances of body knowledge (1–3). Large parietal lesions give rise to classical syndromes such as right-left disorientation (1–3) and autotopagnosia, a deficit in localizing body parts in relation to the whole body (4–6). These syndromes are most often associated with lesions of the left hemisphere. Similarly, epileptic manifestations that accompany parietal-lobe tumors can result in disturbances of the body image, such as absence or displacement of a part of the body, transformation of a limb into a mechanical object, the phantom appearance of a third limb, and the personification of a body part (3). These intriguing phenomena are assumed to result from an impairment in the “body schema” (1–3) that traditional neurological thinking ascribed to the posterior parietal cortex (7).

There is some evidence, based on single-cell recording studies with nonhuman primates, that neuronal activity in the cortex of the superior parietal lobule (area PE) and its rostrally adjacent cortex surrounding the anteriormost part of the intraparietal sulcus (area PF) codes the position and orientation of body parts in relation to each other (8, 9). We hypothesize that these areas, within the broader neural network in which they are embedded, are the essential components underlying body awareness.

This neural system constantly receives information about changing states from the skin and the joints and builds, on this basis, a dynamic and plastic mental representation of the body-in-space. The body is thus placed in a continuous interactive relation with the external world. This dynamic interaction allows for the simulation of continuous spatiotemporal trajectories of body motion and specifies how one's future posture causally depends on one's current posture. Perhaps the most powerful way of revealing the neural system sustaining such a process is a mental rotation paradigm that constrains the subject to use mental transformations of his body representation. It has been shown that when subjects view drawings of postures of the hand in various orientations and are asked to judge whether it is the left or the right hand that is shown, they make their judgments by imagining their own hand rotating to match the orientation of the presented stimulus (see Fig. 1) (10–12). In such studies, reaction time (RT) is a

function of the angle of orientation of the stimulus, reflecting this spatial transformation (10–12). The successful use of this paradigm in a functional neuroimaging study is critically dependent on the constant engagement of the subject in mental rotation of his body during the scanning period. A psychophysical experiment was therefore carried out in order to select the most demanding stimuli, in terms of mental rotation, for the positron emission tomography (PET) study. This study was presented at the 1994 European Society for Neuroscience meeting (13).

METHODS

Psychophysical Experiment. The purpose of this experiment was to select the orientations that were the most difficult, in terms of mental rotation, for each one of the hand postures that were to be used in the subsequent PET experiment. The psychophysical experiment was carried out on 10 male right-handed subjects (21–29 years of age; mean age, 25 years). Handedness was assessed by means of the Edinburgh handedness inventory (14).

Each subject was presented with a photograph of the left or the right hand in a particular orientation and had to decide whether the hand presented was the left or the right one (Fig. 1). The stimuli were photographs of 11 different natural hand postures of the same male hand. Left and right hands were mirror images of one another. These 11 hand postures (left and right) were presented in 12 orientations defined by their clockwise rotation from the upright position: 0°, 30°, 60°, 90°, 120°, 150°, 180°, 210°, 240°, 270°, 300°, and 330°. The stimuli were displayed, one at a time, on a computer screen within a circular field (see Fig. 1) and the subject indicated his response by pressing the left or the right key of a mouse. RTs were measured from the onset of the stimulus to the key response. The interstimulus interval was 2 sec. Each stimulus subtended $\approx 11^\circ$ of visual angle.

A set of eight practice trials was administered at the beginning of the experimental session. The subjects performed four experimental blocks in two sessions. Each block consisted of 264 stimuli (11 postures \times 12 orientations \times 2 left/right positions). Each hand posture in both the left and the right position and in each orientation occurred in a random order within each block. The mean RTs for the correct responses were computed for each posture, for the left and right hand, and for each orientation.

A three-way analysis of variance (hand posture \times left/right position \times orientation) for repeated measures was performed on the group data. There were significant main effects of hand posture ($F_{(10,90)} = 13.68$; $P < 0.00001$) and orientation ($F_{(11,99)} = 7.97$; $P < 0.00001$). The three-way interaction (hand posture \times left/right position \times orientation) was also significant ($F_{(110,990)} = 1.49$; $P < 0.0001$). It should be noted that, with Greenhouse-Geisser correction for heterogeneous

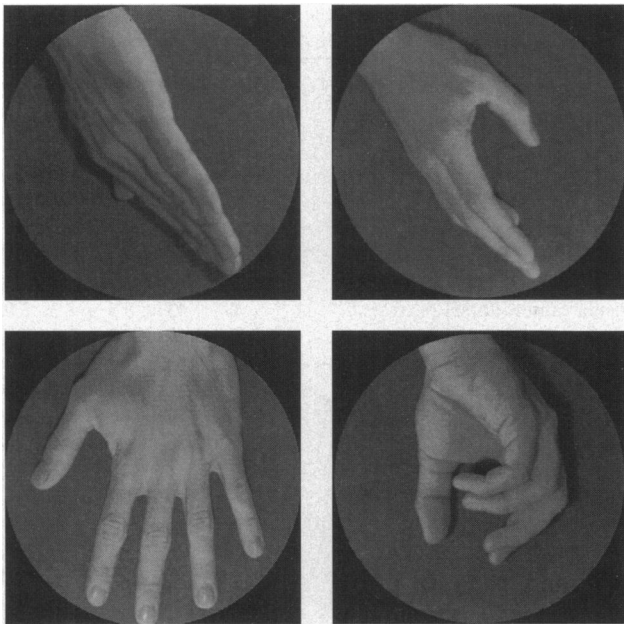


FIG. 1. Examples of four stimuli used in the hands mental rotation condition. (Left) Two examples of the left hand (Upper, 150°; Lower, 180°). (Right) Two examples of the right hand (Upper, 150°; Lower, 150°). Orientations of the hand postures are those that yielded the longest RTs in the psychophysical experiment (see Fig. 2).

covariance, the interaction would not be significant ($P > 0.05$). As shown in Fig. 2, RTs were a function of specific hand posture and orientation.

A questionnaire was administered to each subject at the end of the test. The responses revealed a certain variability in the strategies used by the different subjects. All strategies, however, involved reference to the subject's body by requiring mental rotation of his hand in order to match the orientation of the stimulus shown. Thus, these qualitative reports corroborated the RT patterns.

PET Experiment. Sixteen male volunteer subjects (19–27 years of age; mean age, 22.4 years) participated in this experiment. These subjects were different from the 10 subjects of the psychophysical experiment. All were right-handed as assessed by the Edinburgh handedness inventory (14). Informed consent was obtained from the subjects and the study was approved by the Ethics Committee of the Montreal Neurological Hospital.

Two PET scanning conditions, in a seven-scan PET session, constituted this experiment. The order of presentation of these conditions was counterbalanced across subjects. The stimuli were presented on a computer monitor and the subject's RT and response accuracy were recorded.

One of the five remaining conditions involved scanning while the subjects were constantly articulating the letters "a" and "b" while keeping their eyes open. Since in this condition no visual stimuli were presented on the screen, it could serve as a baseline against which to observe the effect [i.e., cerebral blood flow (CBF) increases and decreases] on parietooccipital function of both the experimental and the control tasks.

Hands mental rotation condition. The aim of this condition was to engage the subjects in challenging mental transformations of the body during the 60-sec scanning period. As in the psychophysical experiment described above, the subjects were presented with a photograph of a hand and had to decide whether the presented stimulus was the left or the right one (Fig. 1). Correct solution of this task requires reference to the body and mental transformation of it. The stimuli used in the PET experiment were strictly selected on the basis of the results of the psychophysical experiment. For each 1 of the 11 hand postures of both the left and the right hand, we selected the two

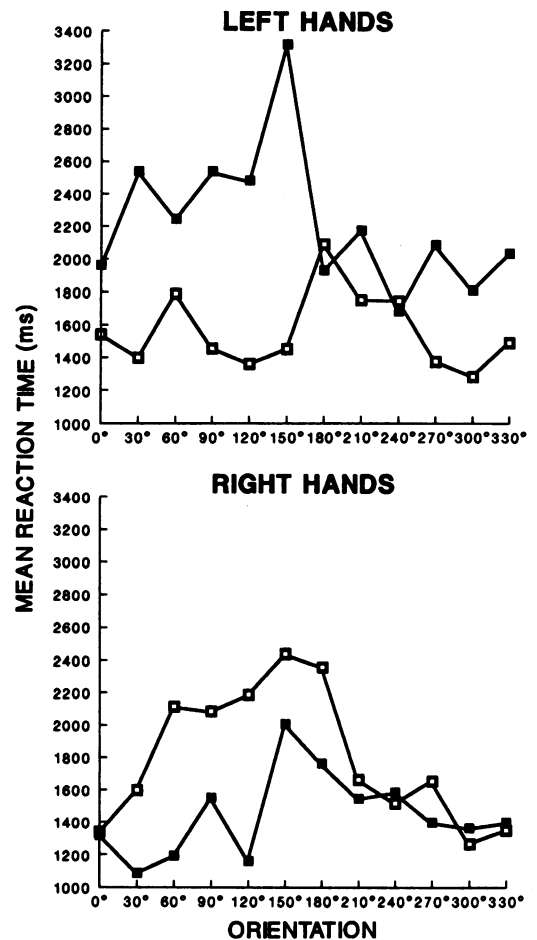


FIG. 2. Mean RTs (msec) as a function of angle of orientation for the left and right hand postures shown in Fig. 1. ■ and □ correspond to the postures shown in Fig. 1 Upper and Lower, respectively.

most difficult orientations—i.e., those producing the greatest RTs across subjects—in the psychophysical experiment. This yielded 44 different stimuli (11 postures \times 2 left/right positions \times 2 orientations), which were presented during the scanning period in a random order. The interstimulus interval was 2 sec. Each stimulus subtended 16.5° of visual angle.

Before scanning and after the instructions had been given, eight practice trials were administered. The stimuli used in the practice trials were different from the 44 stimuli used during the scanning period. The subject's task was to decide whether the stimulus presented was the left or the right hand and to press, with his right hand, the left or the right key of a mouse to indicate his decision. The subjects were told that the next stimulus would automatically be presented if there was no response within 10 sec. No movement of the hand was allowed other than the pressing of the response key. The subjects were surrounded by a black curtain, which occluded the view of their arms. The mean correct response rate was 92% (SD = 0.11) and the mean RT for correct responses was 2777 msec (SD = 1114 msec).

Hands control condition. The requirements of a successful control condition for the hands mental rotation task are (i) the use of stimuli perceptually equivalent to those of the experimental task, and (ii) the disengagement of the subject's attention from his body and its focusing on the stimuli as objects in the external world. The same type of stimuli—i.e., photographs of hand postures—were used in the control condition and the subjects were now required to monitor from memory the presentation of these stimuli rather than to refer mentally to their body. The stimuli were eight hand postures, different from those used in the hands mental rotation con-

dition. The subjects familiarized themselves with these eight photographs prior to scanning. During scanning, seven of these eight stimuli were constantly presented, one at a time in a random order, and the subjects were required to monitor their presentation in order to identify, at the end of the scanning period, the stimulus not presented. The subjects were also instructed to press on the response key with their right hand every time a stimulus appeared on the screen. Identification of the missing stimulus, tested after the scan, was 100% correct.

PET and Magnetic Resonance Imaging (MRI) Data Acquisition and Analysis. PET scans were obtained with a Scanditronix PC-2048B tomograph, which produces 15 image slices at an intrinsic resolution of $5.0 \times 5.0 \times 6.0$ mm (15). The regional distribution of CBF in experimental and control scanning conditions was measured by means of the water bolus $H_2^{15}O$ methodology (16) during 60-sec scanning conditions. Each subject also underwent a high-resolution MRI scan (160 slices; 1 mm thick) obtained with a Philips ACS system (1.5 T). The MRI volumes were coregistered with the PET data (17) and each matched pair of MRI and PET data sets was linearly resampled into a standardized stereotaxic coordinate system (17, 18). The PET images were reconstructed with a 20-mm Hanning filter to overcome residual anatomical variability. PET data were normalized for global regional CBF (rCBF) and averaged across subjects for each activation state, and the mean rCBF difference image volume was obtained (17). This volume was converted to a *t*-statistic volume by dividing each voxel by the mean SD in normalized CBF for all intracerebral voxels (19). Individual MRIs were subjected to the same averaging procedure, such that composite MRI and PET volumes were merged to localize *t*-statistic peaks (20).

The statistical significance of focal changes was tested by a method based on three-dimensional Gaussian random field theory (19). For an exploratory search involving all peaks within the gray matter volume of 600 ml, the threshold for reporting a peak as significant was set at $t = 3.5$, corresponding to an uncorrected probability of $P < 0.0002$ and a corrected false positive rate of 0.58 per volume (19). For predicted blood flow changes in particular brain areas, the threshold for significance was set at $t = 3.00$, corresponding to an uncorrected probability of $P < 0.0013$.

RESULTS

The question whether there would be significant activity within the cortex of the superior parietal lobule and the rostralmost part of the inferior parietal lobule in relation to the performance of the hands mental rotation task was examined by subtracting CBF in the hands control condition from that in the hands mental rotation condition. As shown in Table 1, there was significant bilateral activity within the superior parietal lobule (area PE) (Fig. 3). In the left hemisphere, activity in the superior parietal lobule extended into the middle part of the intraparietal sulcus as well as into its most anterior part (Fig. 4) involving the ventrally adjacent area PF. There were no significant peaks in the cortex of the posterior inferior parietal lobule (see Table 1).

For the parietal cortex, the cytoarchitectonic terminology of Economo (21) is adopted. The cortex of the superior parietal lobule is occupied by area PE. A part of area PE extends into the medial bank of the intraparietal sulcus. The rostralmost part of the inferior parietal lobule is occupied by cortical area PF (i.e., rostral area 40). In Brodmann's map, the rostral part of area PE is referred to as area 5, whereas its caudal extension is referred to as area 7, a term also used, mainly in the monkey, for the inferior parietal lobule.

To examine the possibility that the CBF increases within the parietal cortex (in the hands mental rotation minus hands control task subtraction) might have been due to decreases in this region in the control task, we subtracted the baseline

Table 1. Significant CBF changes in the hands mental rotation task

Brain area	Stereotaxic coordinate			<i>t</i> value	
	<i>x</i>	<i>y</i>	<i>z</i>		
Hands mental rotation minus hands control condition					
Anterior intraparietal sulcus (area PF)	L	-46	-30	42	6.10
Middle intraparietal sulcus	L	-36	-50	59	3.53
Caudal superior parietal lobule (area PE caudal)	L	-16	-61	59	4.58
	R	25	-59	66	5.13
Insula (anterodorsal part)	L	-43	5	3	3.05
	R	39	15	3	3.75
Premotor cortex (caudal area 6)	L	-34	-8	63	4.46
	R	26	-4	62	4.26
Motor cingulate cortex (area 6/32)	R	3	10	44	4.79
Putamen	R	28	-4	8	4.34
Cerebellum	L	-31	-49	-26	3.69
Orbital frontal area 47	R	26	20	-23	4.51
Perirhinal cortex (area 36 near 20)	R	32	5	-36	3.84
Subcallosal cortex (area 25)	R	3	13	-14	4.37
Prestriate cortex (area 18)	R	16	-85	-5	3.60
Prestriate cortex (area 19)	L	-46	-81	-8	3.78
	R	50	-78	-3	4.45
Dorsal prestriate cortex (area 19)	L	-38	-80	23	3.70
Ventral prestriate cortex (area 19)	L	-35	-71	-17	6.91
Ventral temporooccipital cortex (area 37)	L	-27	-50	-11	4.94
	R	39	-61	-14	7.25
Hands control minus hands mental rotation condition					
Middle temporal cortex (area 21)	L	-64	-26	-11	4.45
	R	66	-25	-12	3.96
Ventrolateral frontal cortex (area 45)	L	-46	25	18	3.53
Posterior dorsolateral frontal cortex (area 8)	L	-30	20	45	4.47
	R	32	22	51	5.59
Dorsolateral frontal cortex (area 8/9)	R	40	29	35	4.54
Frontopolar cortex (area 10)	L	-32	56	-3	5.34
	R	29	63	6	4.95
Posterior inferior parietal cortex (area 40/39)	L	-47	-54	35	4.25
	R	46	-57	30	4.32
Inferior parietal cortex (area 7/40)	L	-40	-63	44	3.89
	R	44	-66	39	4.62
Inferior parietal cortex (area 40)	R	55	-45	42	3.45
Medial parietal cortex (area 7)	R	1	-66	41	4.13
Posterior paracingulate cortex (area 31)	R	4	-59	26	4.12
Posterior cingulate cortex (area 23)	L	-5	-26	27	5.03

Stereotaxic coordinates (in mm) refer to peaks of statistically significant (see text) changes in normalized CBF. *x*, Medial-to-lateral distance relative to the midline (positive = right); *y*, anterior-posterior distance relative to the anterior commissure (positive = anterior); *z*, superior-inferior distance relative to the anterior commissure-posterior commissure line (positive = superior). L, left; R, right.

condition from each one of these tasks. In both these subtractions, there were no significant negative peaks in the parietal or the parietooccipital region. Significant positive peaks were in fact observed within the parietal cortex (baseline minus experimental condition: $-42, -37, 45$; $t = 8.8, -23, -68, 53$; $t = 7.4, 28, 66, 44$; $t = 8.00, -39, -50, 57$; $t = 6.9, 40, -50, 51$; $t = 6.7$; baseline minus control condition: $-35, -59, 45$; $t = 8.00, 35, -62, 44$; $t = 9.00, -47, -49, 59$; $t = 4.3, 40, -56, 45$; $t = 8.7$). These results indicate that the parietal increases observed in the experimental minus control subtraction were due to the additional requirements of the hands mental rotation task and were not secondary to decreases in the control task.

Significant activity was also observed, in the hands mental rotation minus hands control subtraction, in the anterodorsal part of the insula. This part of the insula is characterized by a dysgranular type of cortex similar to that observed in the nearby

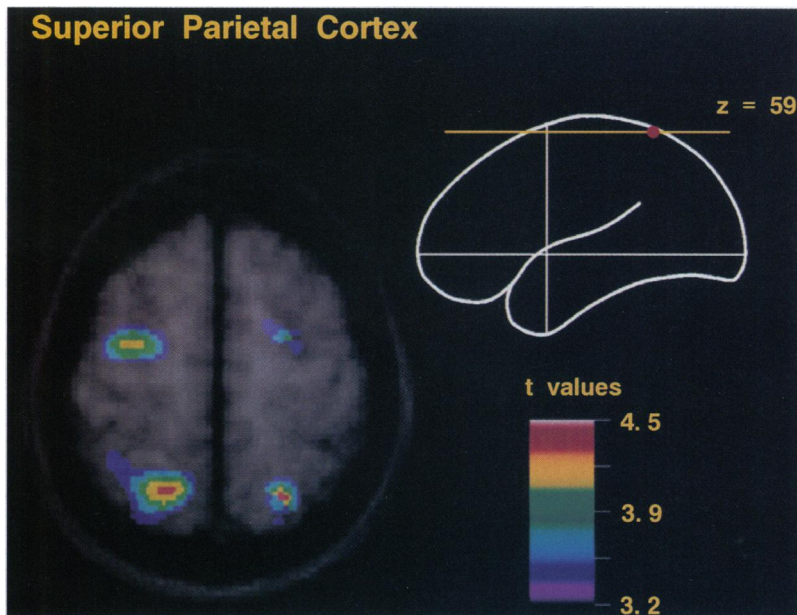


FIG. 3. Horizontal merged PET-MRI section at $z = 59$ to illustrate activity in the superior parietal lobule (area PE). The subject's left is on the left side in this section.

precentral opercular region (20). Other significant CBF foci were noted in cortical and subcortical motor structures: the premotor cortex (caudal area 6), the cingulate motor areas (area 32 at the level of medial area 6), the putamen, and the cerebellum.

Table 1 also shows the results of the hands control minus hands mental rotation subtraction. Given the mnemonic requirements of the control task, activity was observed in the lateral frontal cortex and the middle temporal area 21, consistent with previously reported results of the involvement of these areas in working memory tasks (22). Note that, in this subtraction, significant CBF changes were observed in the posterior inferior parietal lobule and not in the posterocaudal superior parietal cortex.

DISCUSSION

The aim of the present study was to investigate the hypothesis that the superior parietal cortex (area PE) and the rostralmost

part of the inferior parietal lobule (area PF) are components of a neural system underlying a constantly updated representation of the body-in-space. A paradigm requiring mental rotation of the subject's body was used to investigate this issue. In the hands mental rotation condition, in relation to the control, there was bilateral activity in the cortex of the superior parietal lobule (area PE) and in the anterodorsal part of the insula. In the left parietal cortex, activity extended into the middle part of the intraparietal sulcus and, in its anterior part, into the nearby area PF. These findings bear a striking similarity with the anatomical connectivity patterns of area PE in the monkey; area PE is directly linked with the insula (23) as well as the anterior part of the intraparietal sulcus (24).

The findings are also in agreement with single-cell recording work in macaques, which has shown that neurons in the superior parietal lobule integrate inputs from the primary somatosensory cortex to build complex representations of body postures (8, 25).

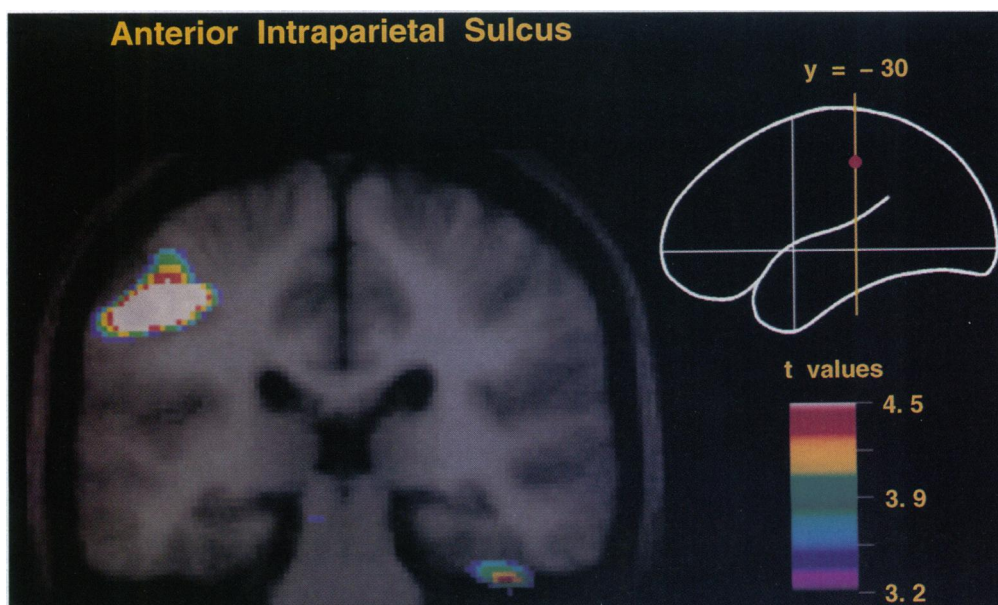


FIG. 4. Coronal merged PET-MRI section at $y = -30$ to illustrate activity within the anterior part of the intraparietal sulcus. The subject's left is on the left side in this section.

These neurons, unlike those in primary somatosensory cortex, respond in relation to specific complex postures of the animal's body. For example, a neuron might respond to a right elbow flexion and shoulder elevation, bringing the right hand in contact with the left shoulder (8). Neurons in areas PE and PF discharge at high rates when the animal projects his arm into the immediate extrapersonal space that surrounds him ("arm projection neurons") (25). In addition, it has been suggested that the kinematics (spatial parameters) of movement, but not its dynamics (forces required to produce movement), may be coded in the cortex of the superior parietal lobule (26). The present PET findings further demonstrate the involvement of these areas in imaginary spatiotemporal projections of the body as a whole in space, reflecting the internalized constraints of kinematic geometry (27).

By contrast to the superior parietal lobule (area PE) and the rostral inferior parietal lobule (area PF) that process complex somatosensory information (8, 9), neuronal activity in the posterior inferior parietal lobule has been shown to be involved in visuospatial and oculomotor functions (25, 28). These somatosensory and visuospatial fields of the parietal lobe converge around the region of the intraparietal sulcus. The tip of the intraparietal sulcus, which has been activated in the mental rotation task, receives a major vestibular input (29, 30). In the monkey, it has been shown that neuronal activity within the intraparietal sulcus converts the retinal coordinates of visual stimuli into a body-centered frame of reference (28). Thus, in the present experiment, the activity observed within the intraparietal sulcus may underlie continuous mental transformations between body-centered frames of reference and external ones.

An earlier PET study (31) reported activation of the superior parietal cortex, close to the intraparietal sulcus, in relation to the shifting of attention in visual space. The task required the subject to shift attention to stimuli appearing on his left or his right side, which would necessarily be based on transformations between the immediate peripersonal space and a body-centered frame of reference. These findings are therefore consistent with the present ones when considered in the context of the known anatomical and physiological organization of the parietal cortex.

Note that the activity within the intraparietal sulcus and its extension to adjacent area PF was restricted in the left hemisphere (Fig. 4). Activity in the left intraparietal sulcus, but not the superior parietal cortex and area PF, has also been reported to be involved in the process of mental rotation of three-dimensional objects (32). The clinical evidence that certain body disorders (e.g., autotopagnosia or ideomotor apraxia) follow almost exclusively left parietal lesions may be viewed as disruptions of functional mechanisms embedded in the left intraparietal sulcal cortex and its related areas.

The finding of significant activity in the cortex of the insula (Fig. 4) is particularly interesting in view of the current concepts of the function of this cortical region. Anatomical (33) and physiological (34) evidence has strongly suggested that the insula, in interaction with limbic structures, is involved in the higher levels of somatic function, by analogy with the inferotemporal cortex for vision (33, 35). Neurons in the insula respond to somatosensory information with complex properties, some responding to the whole body (34). Lesions of the insular region have been reported to provoke somatic hallucinations (36). In a striking example, Penfield (37) reported that electrical stimulation near the insula in a patient undergoing surgery for epilepsy resulted in illusions of changes in body position and feelings of being outside of his body, rather than in purely sensory experiences.

The mental rotation of body parts also resulted in increases in rCBF in areas that are known to be directly involved in the execution of movements, such as the premotor cortex, the cingulate motor cortex, the putamen, and the cerebellum. This finding is consistent with other reports of activity in these areas

in relation to motor imagery (38, 39). Note, however, that in a task in which the subjects were required to imagine grasping an object, the premotor and motor cingulate areas were activated but not the superior parietal cortex (38). Thus, mental simulation of movement that focuses attention on particular effector systems will activate primarily motor structures. The superior parietal cortex, including the anterior part of the intraparietal sulcus, will be engaged when representation of dynamic relations of body and external space is required.

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