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Cerebral Processes Related to Visuomotor Imagery and Generation of Simple Finger Movements Studied with Positron Emission Tomography

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Positron emission tomography was used to compare the functional anatomy of visual imagination and generation of movement. Subjects were asked to generate visual images of their finger movement in response to a preparatory signal. Four conditions were tested: in two, no actual movement was required; in the other two, a second signal prompted the subjects to execute the imagined movement. Which movement to imagine was either specified by the preparatory stimulus or freely selected by the subjects. Compared with a rest condition, tasks involving only imagination activated several cortical regions (inferoparietal cortex, presupplementary motor area, anterior cingulate cortex, premotor cortex, dorsolateral prefrontal cortex) contralateral to the imagined movement. Tasks involving both imagination and movement additionally increased activity in the ipsilateral cerebellum, thalamus, contralateral anteroparietal, and motor cortex and decreased activity in the inferior frontal cortex. These results support the hypothesis that distinct functional systems are involved in visuomotor imagination and generation of simple finger movements: associative parietofrontal areas are primarily related to visuomotor imagination, with inferior frontal cortex likely engaged in active motor suppression, and primary motor structures contribute mainly to movement execution.

Key Words: **human; motor imagery; pre-SMA; cerebellum; motor cortex.**

INTRODUCTION

The beneficial effects of imagining movements on motor learning and performance (Mendoza and Wichman, 1978; Noel, 1980; Yue and Cole, 1992) suggest that motor imagery is functionally close to preparatory and executive motor processes. This contrasts with the view that mental imagery is an amodal phenomenon, by which knowledge can be expressed in an abstract representation (Jeannerod, 1994). If imagination and generation of movement really share a common physiological substrate, then it should be possible to demonstrate that similar neural structures are involved in both processes. Several functional imaging studies have addressed the question of the neuroanatomical substrate of motor imagery. Roland *et al.* (1980) showed that mental rehearsal of a finger movement sequence activated the supplementary motor area (SMA), whereas the execution of the same sequence activated both the SMA and the sensorimotor cortex. Fox *et al.* (1987) and Stephan *et al.* (1995) confirmed that the rolandic region was significantly activated only during executed movements, as was the cerebellum. On the other hand, functional magnetic resonance imaging (fMRI) (Leonardo *et al.*, 1995; Porro *et al.*, 1996; Roth *et al.*, 1996) and electrophysiological data (Beisteiner *et al.*, 1995; Lang *et al.*, 1996) have suggested some activation of the sensorimotor cortex during imagination of movements. In addition, cerebellar activation has been shown in relation to pure imagination of complex motor actions (Decety *et al.*, 1990; Ryding *et al.*, 1993, Parsons *et al.*, 1995). Motor imagery has also been associated with an increase of premotor and prefrontal activity (Fox *et al.*, 1987; Decety *et al.*, 1990; Rao *et al.*, 1993; Tyszka *et al.*, 1994; Leonardo *et al.*, 1995; Parsons *et al.*, 1995). Thus, the degree of coincidence between the neural structures involved in motor imagery and motor generation remains controversial.

The tasks used by different investigators must be clearly defined for proper comparison of cerebral activation during motor imagery and execution. In particular, the nature of the motor images has rarely been described precisely in previous studies. Indeed, as emphasized by Jeannerod (1995), two kinds of mental repre-

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sentations of the self in action can be generated: internal or kinesthetic images, corresponding to the kinesthetic representation of the action from within (first-person process) and external or visual images, involving a visuospatial representation of the action (third-person process). It is conceivable that distinct neural systems underlie those two motor imagery processes, leading to confusion in the interpretation of available neuroimaging studies. Only recently Porro *et al.* (1996) explicitly examined the functional substrate of kinesthetic motor imagery, as compared with actual motor performance, and observed overlapping neural networks in sensorimotor areas for both processes. Another important factor is the mode of selection of the motor response. Different brain systems have been proposed for self-generated and stimulus-driven actions (Goldberg, 1985; Passingham *et al.*, 1989; Passingham, 1993), and distinct cerebral activity has been observed in relation to the preparation and execution of the two types of responses (Deiber *et al.*, 1991, 1996). Thus, the possibility exists that imagery of movement differs according to the mode of selection of response.

Our objective in this positron emission tomography (PET) study was to examine the functional processes related to visual imagination of movement. Subjects were asked to visualize mentally their fingers moving (third-person process). We refer to this type of imagery as visuomotor imagery, corresponding to the external imagery of movement described by Jeannerod (1995). Visuomotor imagery alone was compared with visuomotor imagery followed by motor execution in order to assess the amount of overlap between the two processes. Motor execution is taken in the broad sense, including related aspects such as motor preparation. In addition, we were interested to know the extent to which the mode of response selection (self-generation or stimulus-driven generation) could affect the visuomotor imagery process. Preliminary results have been reported elsewhere (Deiber *et al.*, 1995).

SUBJECTS AND METHODS

We studied 10 normal volunteers (4 women and 6 men), age 21 to 53 (mean, 35.1) years. All were right-handed as measured by the Edinburgh Inventory (Oldfield, 1971). The protocol was approved by the Institutional Review Board, and all subjects gave their written informed consent for the study.

Experimental Design

For each subject, 10 PET scans of regional cerebral blood flow (rCBF) were performed sequentially using the tracer $H_2{}^{15}O$. Only 5 of the 10 scans were related to the present study. During scanning, the subjects either only visually imagined finger movements or visually imagined, and, with the right hand, executed finger movements as briskly and as large as possible. The latter task was designed to isolate the executive component by controlling the visuomotor imagery process. The paradigm was derived from a previous study (Deiber *et al.*, 1996). There were two movement variables, finger type (index finger or little finger) and movement direction (abduction or elevation), so that four movements were possible: index finger abduction, index finger elevation, little finger abduction, and little finger elevation. Instructions about movements were provided by four light-emitting diodes (LEDs) (Fig. 1). A preparatory signal (PS) was presented for 250 ms, followed by a delay period of 2.75 to 5 s in intervals of

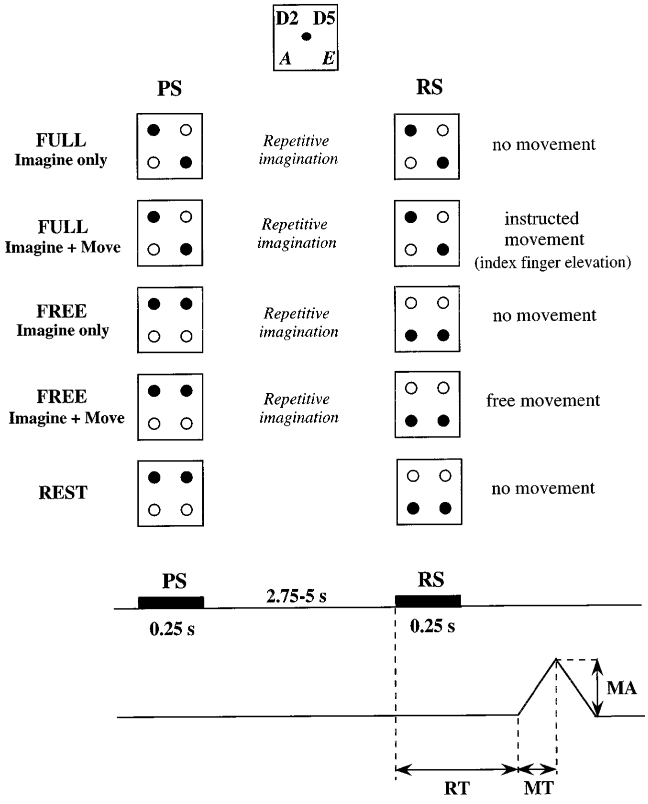

FIG. 1. Schematic diagram of the tasks. In the topmost square, the location of each LED is replaced by the movement components: D2, index finger; D5, little finger; *A*, finger abduction; *E*, finger elevation. For clarity, the eye fixation point is shown only in the topmost square. PS, preparatory stimulus; RS, response stimulus. Filled circles represent illuminated LEDs. In the full condition, the selected example, RS = D2/*E* requires elevation of the index finger. In the free condition, the combination D2/D5 represents the PS, which requires the subject to select the movement of his choice; the combination *A*/*E* represents the RS. In the rest condition, the combinations D2/D5 and *A*/*E* alternate. In all tasks except rest, the subject imagined the movement repetitively during the delay period between the PS and the RS. In movement conditions, the RS prompts the execution of the movement. RT, reaction time, is the time elapsed between the occurrence of the RS and the deflection of the mechanogram; MT, movement time, is the time elapsed between the initial deflection and the peak of the trace; MA, movement amplitude, is the amplitude of the trace from baseline to peak.

250 ms. During the delay period, the subjects were required to imagine the movement of their own fingers repetitively according to the instruction presented by the PS. They could not see their hands during the task, and were told specifically to visualize in their mind the appropriate finger moving in the appropriate direction as many times as they could. A response signal (RS) was then presented for 250 ms. According to the condition, the RS signaled the subject to stop imagining, but to hold the movement or to execute the imagined movement. A total of 2.7 s elapsed after the RS before a new PS was presented. There were eight trials, and therefore in the conditions requiring movements, eight movements were made in a 60-s scan. The timing of events was such as to emphasize the imagery phase in the scanning time of 1 min.

The following five conditions were tested (Fig. 1).

(1) "Full, imagine only." Selection of the movement was instructed by the stimulus; complete information regarding the movement was provided in the PS; at the RS, which was simply a repetition of the PS, the subjects had to stop imagining but to hold the movement.

(2) "Full, imagine and move." Same condition as (1), but at the PS, the subjects had to execute the movement.

(3) "Free, imagine only." Selection of the movement was made by the subjects: they selected one of the four possible movements, randomizing their choice from trial to trial. The PS (two upper LEDs) and RS (two lower LEDs) did not provide any movement information. At the RS, the subjects had to stop imagining but to hold the movement.

(4) "Free, imagine and move." Same condition as (3), but at the RS, the subjects had to execute the movement.

(5) "Rest." The subjects were asked to "blank their mind" as much as possible while the two upper and two lower LEDs were presented alternately.

The order of the five conditions was pseudorandomized between subjects. In order to control for motor output, the sequences in the full condition were made such that each of the four movements was required twice in the eight trials. One day before the PET scan, the subjects were trained on a different version of both the full and the free conditions in which they were asked to prepare their movements in the delay period between PS and RS (Deiber *et al.*, 1996). The aim of the training was to make the subjects familiar with reacting to the PS and RS, but they were not told about visuomotor imagery until the day of the PET scan.

An IBM personal computer was used to control the illumination of the different combinations of the LEDs and to monitor and store the behavioral data. The subject's arm, wrist, and nonmoving fingers were fixed. Linear potentiometers coupled to each of the four movement axes provided a record of the finger displacements, with a sampling frequency of 200 Hz. In the rest and imagine only conditions, as well as in the delay period of the imagine and move conditions, the mechanogram was checked to make sure it remained at baseline level. In the imagine and move conditions, reaction time, movement time, and movement amplitude were calculated off-line using the stored mechanograms (Fig. 1).

Imagination performance was assessed after each scan. The generation of visual images of the movements was controlled by asking the subjects whether they could "see" their fingers moving. All of them answered positively. The subjects estimated their performance by answering the following questions: (1) How easy was it to imagine your movement (1 very hard, 10 very easy)? (2) How easy was it to switch from imagining to hold or make the movement (1 very hard, 10 very easy)? (3) How many movement repetitions were you able to imagine per trial in the delay period between the PS and the RS?

Data Acquisition

PET scanning of the brain was performed using a Scanditronix PC2048-15B tomograph (Uppsala, Sweden). Fifteen parallel transaxial planes of data separated by 6.5 mm (center-to-center) were acquired simultaneously (full width at half maximum: 6.5 × 6.5 × 6.5 mm after reconstruction). Emission scans were attenuation corrected with a transmission scan collected before each session during the exposure of a 68Ge/68Ga external rotating source. A thermoplastic mask molded to each subject's head and attached to the scanner bed minimized head movements. After a 30-mCi bolus injection of $H_2{}^{15}O$, scanning was started when the brain radioactive count rate reached a threshold value and continued for 60 s. Integrated radioactivity accumulated in the 60 s of scanning was used as an index of rCBF. Ten minutes elapsed between each injection. The scanning room was semidarkened, and the subjects' ears were plugged.

Data Analysis

Calculations and image matrix manipulations were performed in PROMATLAB (Mathworks Inc., Sherborn, MA) on a SPARC 10 computer (Sun Microsystems, Mountain View, CA) with software for image analysis (ANALYZE, Biodynamic Research Unit, Mayo Clinic, Rochester, MN; SPM, MRC Cyclotron Unit, London, UK). The scans from each subject were realigned, with the first scan as a reference. The six parameters of this rigid body transformation were estimated using a least squares approach (Friston *et* *al.*, 1995a). Following realignment, all images were transformed into a standard anatomical space (Talairach and Tournoux, 1988). The spatial normalization involves linear and nonlinear three-dimensional transformations to match each scan to a reference image that already conforms to the standard space. Images were then smoothed with an isotropic Gaussian kernel (15 mm full width at half maximum). After the appropriate design matrix was specified, the condition, subject, and covariate effects were estimated according to the general linear model at each voxel (Friston *et al.*, 1995b). To test hypotheses about the specific regional effects of the condition, the estimates were compared using linear contrasts. The resulting set of voxel values for each contrast constitutes a statistical parametric map of the t statistic (SPM$\{t\}$). The SPM$\{t\}$ were transformed to the unit normal distribution (SPM$\{Z\}$), thresholded at 3.09, and corrected for multiple comparisons ($P < 0.05$). The resulting foci were then characterized in terms of peak height (u) and spatial extent (k). The significance of each region was estimated using the probability that the peak height observed could have occurred by chance [P ($Z_{\max} > u$)] or that the observed number of voxels could have occurred by chance [P ($n_{\max} > k$)] over the entire volume analyzed (Friston *et al.*, 1994).

Planned comparisons between conditions were made within each of the full and free modes of movement selection. The effect of pure imagination of movement on brain activity was assessed by comparing the imagine only conditions with the rest condition. The effect of imagination followed by execution of movement was assessed by comparing the imagine and move conditions with the rest condition. In the direct comparison of the imagine and move condition with the imagine only condition, rCBF increases reflected activity enhanced by motor execution, whereas rCBF decreases reflected activity suppressed by motor execution. The effect of the movement selection mode on brain activity was assessed by comparing the full and free processes within each condition (imagine only, and imagine and move conditions).

Designation of Anatomical Structures

As described earlier, the procedure used for group analysis of the PET data was based on the resizing of the PET scans to a standard anatomical space (Talairach and Tournoux, 1988). This procedure allowed us to relate coordinates to the cytoarchitectonic labels depicted in the atlas of Talairach and Tournoux (1988). In recognition of the limitations of this technique, we have taken into account both the primary and the subsidiary contrast peaks as detected through SPM and have illustrated the contiguous voxels that exceed a Z statistic of 3.09 for regions showing significant changes in rCBF.

RESULTS

Imagination Performance

Figure 2 shows the subjects' self-estimate of imagination performance. The mean score rating the easiness of imagination was 8.8 across subjects and conditions. The score for switching from imagining to holding the movement was 8 on average, and the score for switching from imagining to executing the movement was 8.8 on average. The number of movement repetitions imagined per trial in the delay period was 4.4 on average, as estimated a posteriori by the subjects, who did not report silent counting during the scan. A repeated-measures analysis of variance (ANOVA), with SELECTION MODE (free, full) and CONDITION (imagine only, imagine and move) as within-subject factors, was performed on each of the three scores of imagination performance (score of imagination, number of imagined repetitions, score of switching). None of the three scores was significantly affected by the CONDITION or the SELECTION MODE (Greenhouse-Geisser corrected).

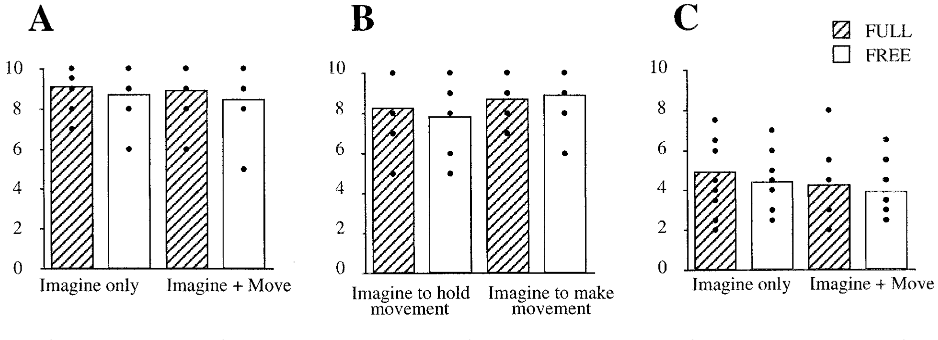

FIG. 2. Self-estimate of imagination performance in two modes of movement selection (full, externally cued; free, internally cued). The black circles represent the individual scores (the number of symbols do not equal the number of patients because of overlap), and the bars show the mean values of 10 subjects. (A) Performance when imagining the movement. (B) Performance when switching from imagining the movement to holding the movement and from imagining the movement to executing the movement. (C) Number of movement repetitions imagined per trial during the delay period. In A and B, the score 0 corresponds to "very hard" and the score 10 to "very easy."

TABLE 1

Reaction Time, Movement Time, and Movement Amplitude in the Movement Conditions

Selection mode	Reaction time (ms)	Movement time (ms)	Movement amplitude (degrees)
Full	388.2 ± 151.9	287.2 ± 103.1	36.5 ± 9.0
Free	370.7 ± 157.0	311.1 ± 116.6	36.8 ± 10.5

Note. Values are mean ± SD.

Movement Performance

Only one movement error was made by one subject in the full condition. Table 1 shows the intersubject means and standard deviations of the reaction time, movement time, and movement amplitude in the imagine and move conditions. A repeated-measures ANOVA, with SELECTION MODE (full, free), FINGER (index, little finger), and DIRECTION (abduction, elevation) as within-subject factors, was performed on each of these three measures (Greenhouse-Geisser correction). The reaction time was not affected by any of the three factors. The movement time was affected by DIRECTION only ($F = 5.406$, $P < 0.05$), with a longer movement time for elevation movements. The movement amplitude was affected by FINGER only ($F = 9.088$, $P < 0.05$), with a larger movement amplitude for index finger movements.

External Mode of Selection (Full)

Imagine only vs rest. Figure 3A shows the significant increases in rCBF in the full imagine only condition with respect to the rest condition. rCBF was

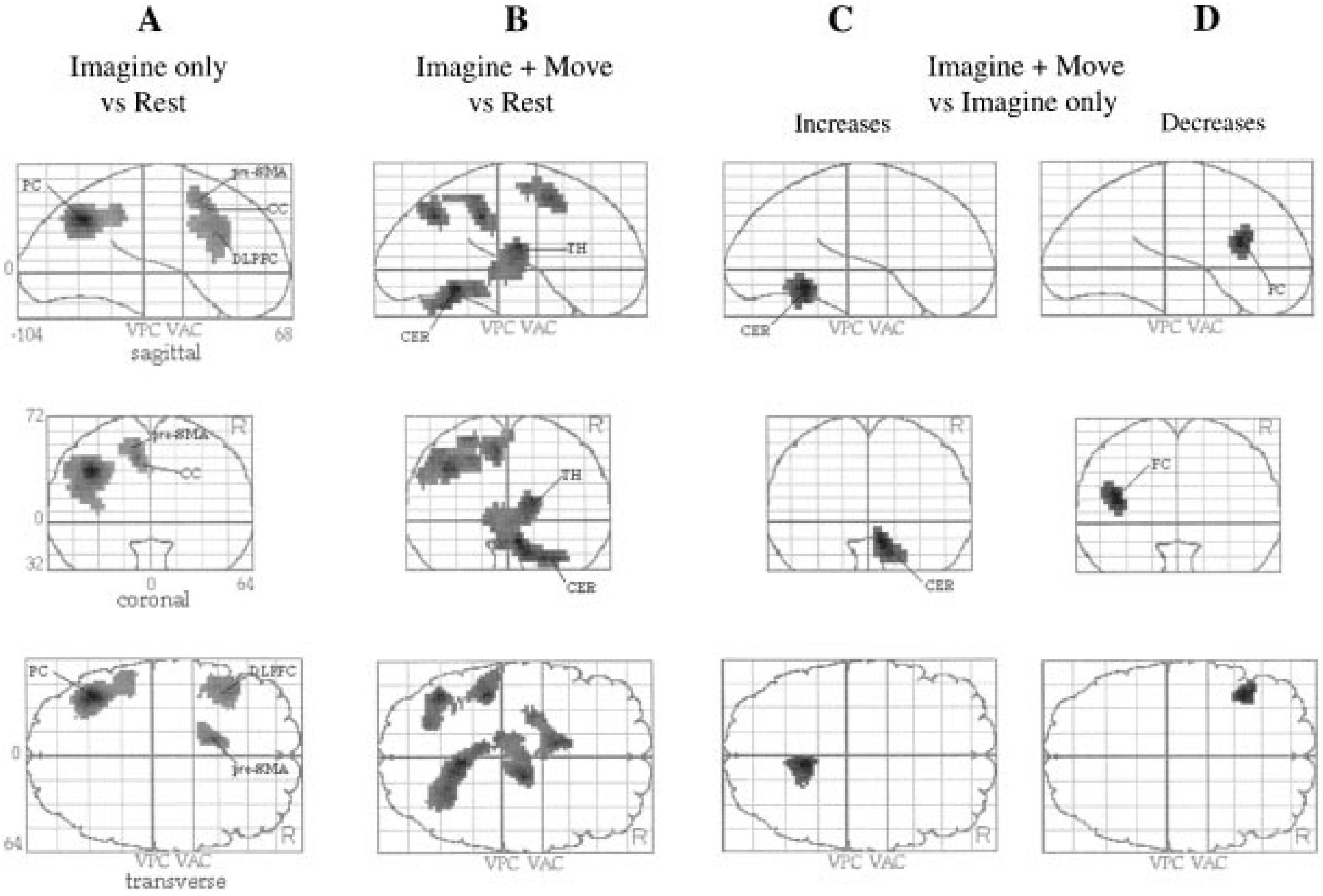

FIG. 3. Statistical parametric maps (SPMs) for the externally cued mode of selection (full). (A) For imagine only versus rest, rCBF increased, contralaterally to the imagined movements, in the inferoparietal cortex (PC), pre-SMA, cingulate cortex (CC), and dorsolateral prefrontal cortex (DLPFC). (B) For imagine and move versus rest, rCBF additionally increased in the right cerebellum (CER) and the thalamus (TH), and the left DLPFC was no longer activated. (C, D) For imagine and move versus imagine only, rCBF increased in the right cerebellum (CER) and decreased in the left inferior frontal cortex (FC), extending dorsally to the DLPFC. The pixels reflecting Z values exceeding the significance threshold of 3.09 with Bonferroni correction for multiple comparisons ($P < 0.05$) are displayed on a gray scale, with the lower Z scores represented in light gray and the higher Z scores represented in dark gray. The SPM is displayed in the anatomical space of Talairach and Tournoux (1988) as a maximum intensity projection viewed from the right side (top row), the back (middle row), and the top (bottom row) of the brain.

TABLE 2

Comparison of the Full Selection Mode Conditions with the Rest Condition

	Talairach coordinates					
Area activated[a]	x	y	z	Z score	Intensity $P(Z_{\max} > u)$	Size $P(n_{\max} > k)$
Imagine only vs Rest						
L Inferoparietal (39/40)	−38	−62	36	6.04	<0.001	<0.001
L Pre-SMA (6)	−10	12	44	4.60	0.012	0.052
[Cingulate (32)]						
L DLPFC (9/46)	−40	20	32	4.37	0.03	0.003
[L Inferior frontal (44/45)]						
Imagine + Move vs Rest						
L Inferoparietal (39/40)	−40	−66	36	4.75	0.007	0.001
L Pre-SMA (6)	−8	6	48	4.42	0.025	0.016
[Premotor (6) and Cingulate (32)]						
R Cerebellum	6	−54	−12	4.97	0.002	0.001
R Thalamus	14	−14	16	4.70	0.008	0.002
Imagine + Move vs Imagine only						
Increases						
R Cerebellum	6	−54	−12	4.50	0.018	0.022
Decreases						
L Inferior frontal (44/45)	−40	22	16	4.28	0.043	0.066

Note. Talairach coordinates and Z score of peak activation. L, left hemisphere; R, right hemisphere.

[a] Numbers in parentheses are Brodmann's areas, and areas in brackets are included in the cluster of activation.

significantly increased in the left inferoparietal cortex (Brodmann's area [BA] 39/40), left pre-SMA (BA 6 rostral to the vertical line passing through the anterior commissure) extending to cingulate cortex (BA 32), and left dorsolateral prefrontal cortex (BA 9/46) extending ventrally to BA 44/45 (Table 2).

Imagine and move vs rest. Figure 3B shows the significant increases in rCBF in the full imagine and move condition with respect to the rest condition. rCBF was significantly increased in the left inferioparietal cortex (BA 39/40), left pre-SMA extending to left premotor (BA 6) and cingulate cortex (BA 32), right cerebellum (vermis and cerebellar nuclei), and right thalamus (Table 2).

Imagine and move vs imagine only. Comparison of the full imagine and move condition with the full imagine only condition showed a single rCBF increase, in the right cerebellar vermis (Fig. 3C and Table 2), and a single rCBF decrease, in the left inferofrontal cortex (BA 44/45) (Fig. 3D and Table 2).

Internal Mode of Selection (Free)

Imagine only vs rest. Figure 4A shows the significant increases in rCBF in the free imagine only condition with respect to the rest condition. rCBF was significantly increased in the left and right parietooccipital cortex (posterior BA 39/40 and BA 19), left pre-SMA extending to left premotor (BA 6) and cingulate cortex (BA 32), right premotor cortex (BA 6/8), and left frontal cortex (BA 9) (Table 3).

Imagine and move vs rest. Figure 4B shows the significant increases in rCBF in the free imagine and move condition with respect to the rest condition. rCBF was significantly increased in the left inferior parietal cortex (BA 39/40), in a central region including the bilateral premotor cortex (BA 6), contralateral motor cortex (BA 4), pre-SMA, and cingulate cortex (BA 32), as well as in the right cerebellar nuclei (Table 3).

Imagine and move vs imagine only. Comparison of the free imagine and move condition with the free imagine only condition showed an increase of rCBF in the left anterior parietal cortex (BA 40) extending to the motor cortex (BA 4). With a lower significance threshold (i.e., $Z = 2.33$ with correction for multiple comparisons), there was an additional rCBF increase in the right cerebellar nuclei. No significant decrease of rCBF was found for this comparison, even with a lower significance threshold.

Comparison between Modes of Selection

Comparison between the modes of selection (full vs free, free vs full) within each condition showed no significant difference in rCBF.

Changes in rCBF with Movement Execution

Significant rCBF changes with movement execution, as observed in the comparison between the imagine and move conditions and the imagine only conditions, are plotted in Fig. 5. Figures 5A–5C shows the pattern of changes in rCBF across scans in the cerebral struc-

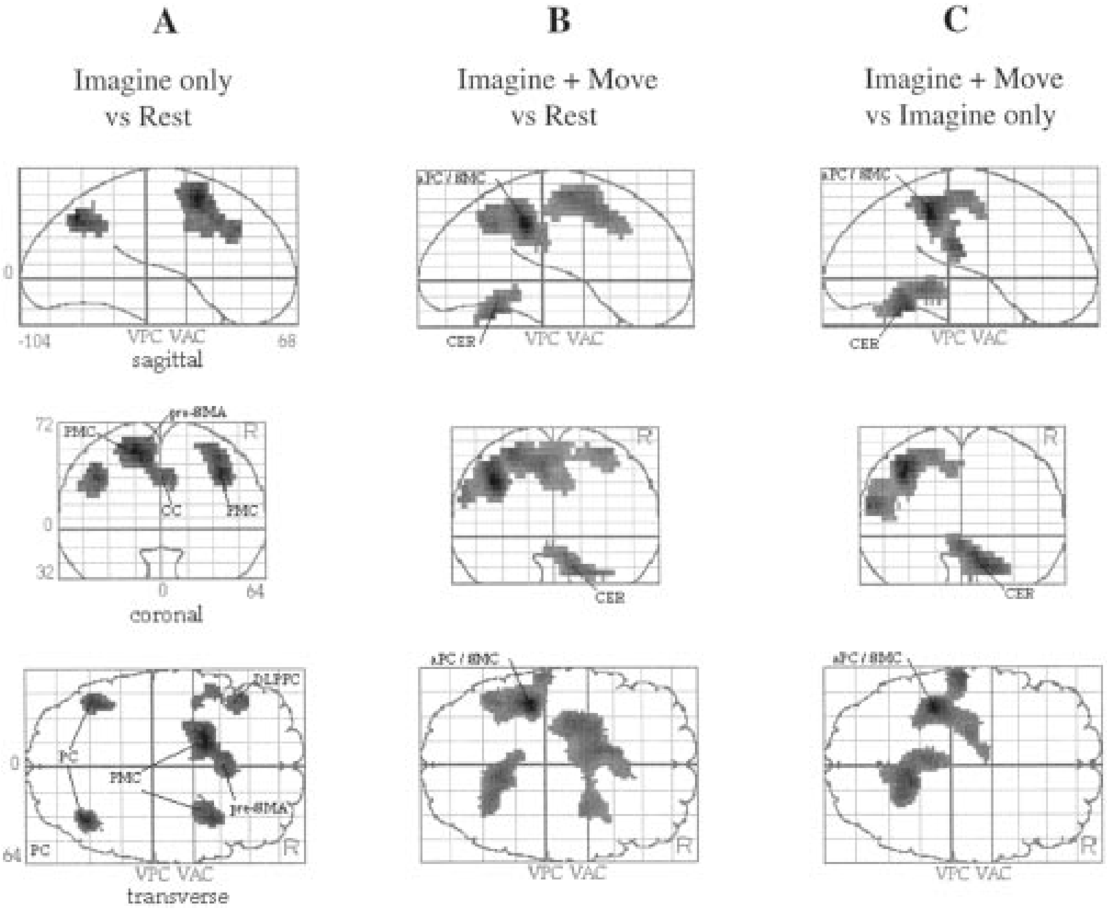

FIG. 4. Statistical parametric maps (SPMs) for the internally cued mode of selection (free). (A) For imagine only versus rest, rCBF increased bilaterally in the occipitoparietal cortex (PC) and the premotor cortex (PMC), contralaterally to the imagined movements in the pre-SMA, the cingulate cortex (CC), and the DLPFC. (B) For imagine and move versus rest, rCBF additionally increased in the right cerebellum (CER) and the left anterior parietal cortex, including the sensorimotor cortex (aPC/SMC). (C) For imagine and move versus imagine only, rCBF increased in the contralateral anterior parietal cortex, including the sensorimotor cortex (aPC/SMC), and in the right cerebellum (CER). Same conventions as in Fig. 3.

tures having increased activity with execution of movement. In the cerebellum (Fig. 5A), the rCBF increase was substantial for both modes of movement selection. The rCBF increase in the anterior parietal cortex (Fig. 5B) and in the motor cortex (Fig. 5C) paralleled the cerebellar increase, although it was significant only in the free mode. Figure 5D shows the pattern of changes in rCBF across scans in the left inferior frontal cortex, where the activity in the full mode was significantly reduced with movement execution.

DISCUSSION

Comments about the paradigm are useful before detailed discussion of the results. It is probable that, except in the rest condition, the tasks under study contained a selective attention component. With the exception of the anterior cingulate cortex, the areas activated with visuomotor imagery do not correspond to the specialized cortical areas constituting the anterior and posterior attention systems (Posner and Dehaene, 1994). However, we cannot rule out the possibility that the attentional load had further enhanced the cortical activity observed in relation to visuomotor imagery. Another inherent difficulty of such imagery experiments is the lack of a behavioral index with which to assess imagination performance. We collected introspective information by inviting the subjects to answer specific questions after each scan. Overall, the high scores obtained in response to these questions suggest that the subjects could satisfactorily generate visual images of their movements.

Visuomotor Imagination

We compared the two conditions with visuomotor imagery (full and free), but without movement execution, with the rest condition. Imagination-related acti-

TABLE 3

Comparison of the Free Selection Mode Conditions with the Rest Condition

Area activated[a]	Talairach coordinates				Intensity	Size
	x	y	z	Z score	$P(Z_{\max} > u)$	$P(n_{\max} > k)$
Imagine only vs Rest						
L Parietooccipital (39/40, 19)	−42	−64	36	4.58	0.013	0.073
R Parietooccipital (39/40, 19)	36	−68	40	4.99	0.002	0.072
L Pre-SMA (6) [Premotor (6), Cingulate (32)]	−16	6	52	4.98	0.002	0.001
R Premotor (6/8)	34	8	48	4.42	0.025	0.027
L Frontal (9)	−42	30	32	3.97	0.127	0.045
Imagine + Move vs Rest						
L Inferoparietal (39/40)	−38	−38	36	6.06	<0.001	<0.001
L Premotor 6 [Pre-SMA (6), Cingulate (32), Motor (4)]	−22	0	52	4.89	0.004	<0.001
R Cerebellum	10	−54	−20	4.77	0.006	0.006
Imagine + Move vs Imagine only						
L Anteroparietal (40) [Motor (4)]	−38	−38	40	4.40	0.027	0.01
R Cerebellum	12	−52	−20	4.04	0.1	0.047

Note. Talairach coordinates and Z score of peak activation. L, left hemisphere; R, right hemisphere.

[a] Numbers in parentheses are Brodmann's areas, and areas in brackets are included in the cluster of activation.

[b] Z threshold = 2.33, with correction for multiple comparisons.

vation was found mainly in the left inferoposterior parietal lobe (BA 39/40), pre-SMA, cingulate cortex (BA 32), and prefrontal cortex (BA 9/46). In the free mode of selection, additional activation was found bilaterally in the most caudal part of the inferior parietal lobe, near its border with the occipital cortex (BA 39/19), as well as in the premotor cortex (BA 6/8).

The activation of the pre-SMA in visual imagination of movement is of particular interest. Note that the clusters of activation include the dorsocaudal portion of the anterior cingulate cortex (BA 32), as well as part of the contralateral premotor cortex (BA 6). We discuss these three distinct cytoarchitectonic areas separately, although their common participation in the same function is likely, as suggested below. The finding of pre-SMA activity with both types of movement selection supports the hypothesis that it is primarily related to the process present in both conditions (i.e., movement imagination). In humans, the pre-SMA has been defined as the aspect of medial area 6 rostral to the vertical line passing through the anterior commissure (Passingham, 1993). In contrast with the SMA proper, which is mostly active with movement execution, the pre-SMA is thought to be involved in higher motor control (Dum and Strick, 1991; Matsuzaka *et al.*, 1992; Luppino *et al.*, 1993; Halsband *et al.*, 1994; Hikosaka *et al.*, 1996). The present findings support that view and suggest that the imagination of movement is an important aspect of pre-SMA function.

Preferential involvement of the pre-SMA in internal selection of movement, in contrast with stimulus-instructed movement, has been shown in previous rCBF studies (Deiber *et al.*, 1991, 1996). However, in the present study, there was no significant difference between the free (self-generated) and the full (stimulus-driven) conditions regarding activation of the pre-SMA (or of any other cortical area). This finding could suggest that the contribution of the pre-SMA to movement visual imagery is predominant over its specific role in self-generated actions.

To our knowledge, there is no other explicit report of pre-SMA activation in motor imagery. In implicit mental imagery for visual shape discrimination, Parsons *et al.* (1995) have described some SMA activation; however, distinct foci were presented in their Table 1, some of them caudal to the VAC line (SMA proper) and others rostral to it (pre-SMA). Stephan *et al.* (1995) have reported differential activation within the SMA proper during imagination and execution of freely selected joystick movements. These authors may have failed to observe pre-SMA activation during motor imagery, because they used motor preparation as the baseline condition, and the pre-SMA is active in the preparation of freely selected movements (Deiber *et al.*, 1996). On the other hand, the rostrocaudal segregation in the SMA proper for imagined and real movement has been documented by other neuroimaging data (Tyszka *et al.*, 1994; Grafton *et al.*, 1996; Roth *et al.*, 1996). The probable participation of the SMA in imagination of movements has also been suggested by recent electrophysiological studies (Abbruzzese *et al.*, 1996; Cunnington *et al.*, 1996; Lang *et al.*, 1996), but spatial resolution

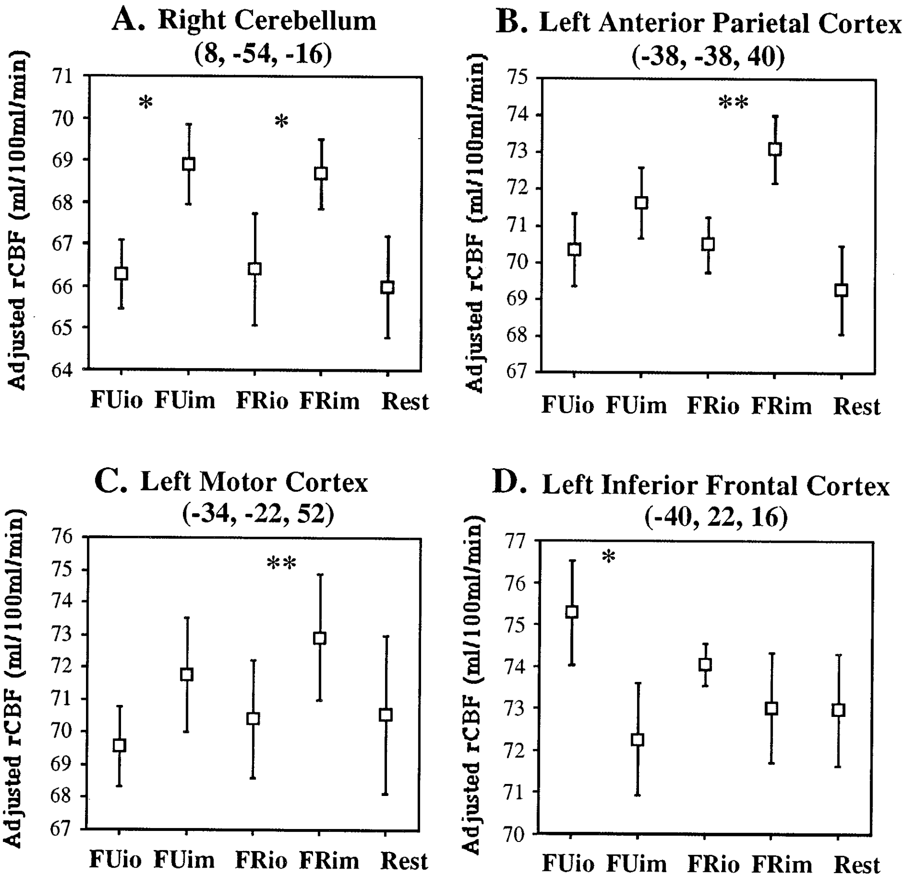

FIG. 5. Grand averages and standard deviations of the adjusted rCBF over the 10 subjects in each condition, in the cerebral structures showing significant activity changes related to motor execution (see Tables 2 and 3). (A, B, C) rCBF increases with execution. (D) rCBF decreases with execution. FUio, full imaging only; FUim, full imagine and move; FRio, free imagine only; FRim, free imagine and move. With correction for multiple comparisons, significant differences at $P < 0.05$ (*) and $P < 0.01$ (**) are indicated. Note that motor cortex is a subsidiary peak within the cluster, the activity of which culminates at the anterior parietal cortex. For the cerebellum, plotting coordinates (x, y, z) correspond to the mean coordinates of peak activation over the full and free conditions.

precludes the distinction between the SMA proper and the pre-SMA. The nature of the motor images could account for the exclusive pre-SMA activation in our study. In previous reports, although the types of motor images studied have generally not been described explicitly, subjects were usually asked to "mentally simulate" (Abbruzzese *et al.*, 1996; Roth *et al.*, 1996), or the task was "imagining the same motion as for actual execution" (Tyszka *et al.*, 1994; Stephan *et al.*, 1995; Grafton *et al.*, 1996). This would refer to kinesthetic motor images, by contrast with visuomotor images studied in the present experiment. Although they did not report them separately, Parsons *et al.* (1995) found some activation foci in the pre-SMA when subjects had to generate mental images implicitly to make covert decisions as to whether a visual stimulus was a right or left hand. It is conceivable that the pattern of activation in the SMA could differ with the type of mental images, with visuomotor images having a greater influence on pre-SMA activity, and with the kinesthetic images on SMA proper activity. This hypothesis would be compatible with recent neuroanatomical findings suggesting that, unlike the SMA proper, the pre-SMA has access to visual information through its connection with the inferior parietal lobule (Luppino *et al.*, 1993). Further experiments should help to clarify this issue in humans.

We did not find any significant activation of the motor cortex during visual imagination of movement (Tables 2 and 3; Fig. 5C). There is an open debate about the participation of the primary motor and somatosensory areas in motor imagery. Furthermore, recent advances in the organization of the primary motor cortex have suggested a subdivision in area 4 on the basis of anatomy, neurochemistry, and function (Geyer *et al.*, 1996), thus introducing new perspectives in the interpretation of available data. On one side, many PET studies have failed to show any significant involvement of the sensorimotor cortex in motor imagery (Roland *et al.*, 1980, Fox *et al.*, 1987; Stephan *et al.*, 1995; Decety *et* *al.*, 1994; Parsons *et al.*, 1995; Grafton *et al.*, 1996). In contrast, some fMRI studies have reported activation of the sensorimotor cortex with mentally simulated movement (Leonardo *et al.*, 1995; Roth *et al.*, 1996; Porro *et al.*, 1996). This activation, however, was much less than during movement execution. During mental simulation of a finger-to-thumb opposition task, Leonardo *et al.* (1995) reported activity only in isolated voxels in two of five subjects, and Roth *et al.* (1996) found the proportion of activated pixels to be 30% of those activated during actual execution. Using sequential finger-to-thumb opposition movements, Porro *et al.* (1996) found an increase in signal intensity in the motor cortex of 2.1% during motor performance and 0.8% during motor imagery. Besides fMRI studies, some electrophysiological studies have suggested that the primary motor cortex was active during motor imagery. The pattern of DC potentials (Beisteiner *et al.*, 1995) and the magnetic fields related to primary motor cortex activity (Lang *et al.*, 1996) have been shown to be affected by imagination of movement, although to a lesser degree than during actual motor performance. Pascual-Leone *et al.* (1995) observed an enlargement of the cortical motor area targeting the finger flexor and extensor muscles after 5 days of mental practice of a piano exercise. Thus, while the sensorimotor cortex may contribute to movement imagination, its contribution seems rather small, and one would be tempted to conclude that PET is insensitive to such a weak signal, which would explain the negative results cited above, as well as those presented in this study. However, there is also an example of a negative result in fMRI concerning the involvement of the sensorimotor cortex in motor imagery of simple and complex movements (Rao *et al.*, 1993). Our opinion is that factors other than technical limitations could account for an absence of sensorimotor cortex activation. We reiterate the possibility that quantitative as well as qualitative differences in the pattern of cerebral activation could occur with distinct motor imagery processes. To our knowledge, the present study is the first one to examine visual imagery of movement with PET, and the results support the hypothesis that this type of imagery does not recruit the motor cortex. Similar results have been found by Parsons *et al.* (1995), who used an implicit mental imagery task based on evaluation of a visual stimulus, thus probably involving some visuomotor imagery.

Activation of the premotor and inferoparietal cortex with movement imagination has been reported previously (Decety *et al.*, 1990, 1994; Rao *et al.*, 1993; Tyszka *et al.*, 1994; Leonardo *et al.*, 1995; Parsons *et al.*, 1995; Stephan *et al.*, 1995; Roth *et al.*, 1996). These structures are anatomically connected and could be related to the visuospatial memory component of the task. Indeed, in both modes of selection, the subjects had to interpret a spatially coded visual cue in order to start imagining the movement.

The frontal cortex was activated contralateral to the imagined movement in both types of motor selection, as Decety *et al.* (1994) and Parsons *et al.* (1995) also reported. Two general classes of theory can be discerned about the function of the frontal lobe. One class is the working-memory theory, which emphasizes the role of the frontal cortex in short-term maintenance of information in different sensory domains (Goldman-Rakic, 1987, 1995), including the encoding and retrieval of information (Shallice *et al.*, 1994; Tulving *et al.*, 1994). The other class might be termed the response-management theory and focuses on the role of the frontal cortex in the manipulation and use of managerial knowledge for organizing behavior thematically (Grafman 1989, 1995). This perspective has similarities with the view that the frontal lobe is concerned with response selection based on context (Passingham, 1993). Both theories (i.e., working-memory and response selection processes) could account for the frontal activation observed during imagined movements.

The anterior cingulate cortex (BA 32) was activated in all four conditions with imagination. The extent to which this structure is devoted to selective attention or imagination of movement (Frith *et al.*, 1991; Decety *et al.*, 1994; Posner and Dehaene, 1994) remains unclear. Stephan *et al.* (1995) suggested that the dorsorostral portion of the anterior cingulate cortex was preferentially activated by imagining movement, in contrast with the ventrocaudal portion, which is closely related to motor execution. Since their baseline condition was motor preparation, influence of selective attention was probably partially canceled out. The locus of anterior cingulate cortex activation found in our study corresponds to the dorsorostral portion described by Stephan *et al.* (1995). Luppino *et al.* (1993) observed rich interconnections between area 24 c and F6 in the monkey, area 24 c being the equivalent of the human rostral cingulate zone of the cingulate motor areas (including area 32 and rostral area 24) and F6 being the equivalent of the human pre-SMA (Picard and Strick, 1996). Thus, with respect to imagination of movement, the anterior cingulate cortex could be activated parallel with the pre-SMA.

Motor Generation

Two of the four imagination tasks also involved motor execution. With few movements per scan, the paradigm is more likely to emphasize processes taking place during the delay period (i.e., movement imagination) than processes related to movement execution. Subjects reported that imagination performance was similar whether or not a movement had to be performed and that the same number of movements per trial was imagined in conditions with and without movements.

This suggests that the imagery process was matched in conditions with and without movements. We posit that in the present paradigm, the influence of motor generation (including preparation and execution processes) on rCBF was less than that of imagery. Nevertheless, with motor generation, compared with imagining movement only, there is increased activity in the ipsilateral cerebellum, anterior parietal and motor cortex, and decreased activity in the caudal inferior frontal cortex (BA 44/45).

Among the structures shown to be primarily related to motor execution, as opposed to motor imagery, the cerebellum deserves a special comment (Fig. 5A). There is evidence for a role of this structure in cognitive processes (Schmahmann, 1991; Kim *et al.*, 1994; Leiner *et al.*, 1995). In particular, cerebellar activation has been shown in motor imagery paradigms without any actual movement (Decety *et al.*, 1990, 1994; Ryding *et al.*, 1993). The movements to be imagined were complex (tennis actions, object grasping), involving multijoint coordination, in contrast with the simple finger movements required in our study. Moreover Decety *et al.* (1994) asked the subjects to generate internal images, rather than the external images of the present study. Interestingly, the cerebellar activation in those studies was more posterior and more lateral than the one we identified in motor execution. Stephan *et al.* (1995) also failed to show any cerebellar involvement in motor imagery of simple joystick movements. Although PET resolution is limited, our data together with those of the above-mentioned reports support a functional subdivision of the cerebellum, with the medial anterior region (including the vermis) primarily involved in executive processes, and the lateral region (cerebellar cortex) playing a role in programming complex actions.

Anterior parietal cortex (Fig. 5B) and motor cortex (Fig. 5C) were activated with motor generation as opposed to visuomotor imagination in both modes of selection, although these results were significant only for freely selected movements. For the anterior parietal cortex, this observation is similar to the one obtained in a previous study testing motor preparation in both the full and the free modes of selection (Deiber *et al.*, 1996): the encoding/retrieval processes taking place in the free selection mode would especially recruit this parietal region. In the motor cortex, Fig. 5C reveals a slight reduction of mean activity in imagination only compared with rest. This suggests that visual imagination of an instructed movement could cause some deactivation of the motor cortex, thus reducing the net activation induced by motor generation, and consequently minimizing the difference between imagination alone and imagination followed by movement. However, this phenomenon, if genuine, is small in magnitude, and we do not have any certain explanation for it.

Activation in the caudal inferior frontal cortex (BA 44/45) was suppressed by motor execution, but significantly only for the fully instructed condition (Fig. 5D). During visuomotor imagery, subjects are instructed to visualize their movement without actually moving. Therefore, execution of movements must be actively inhibited. The locus of motor inhibition during imagery of movement is not known. If the inferior frontal cortex is involved in suppressing motor executive mechanisms during movement imagination through inhibitory synaptic activity, then its activity should be enhanced during motor imagery and reduced when movement execution is allowed, as we observed. However, suppression of frontal activity was not significant in the execution of freely selected movements, which suggests that other factors might also strongly affect rCBF in the frontal cortex, and interact with the effect of imagination. These factors include self-generation of responses, independent of their covert or overt expression (Passingham, 1993), or encoding and retrieval of responses necessary to allow the subjects to vary the movement from trial to trial (Shallice *et al.*, 1994), or both. There is other suggestion that the frontal cortex could participate in inhibiting motor behavior. In GO/NO-GO tasks, Kawashima *et al.* (1996) showed evidence of right prefrontal activation related to the decision of not to move, and Casey *et al.* (1996) showed that ventral prefrontal activation distinguishes between high and low performing adolescents.

In conclusion, the results of the present study show that the act of generating visual images of simple finger movements failed to cause significant activation of primary motor structures, such as the cerebellum or primary motor cortex. They were activated when movements were executed. In contrast, inferior frontal rCBF was suppressed with movement execution, and the pre-SMA was activated with visuomotor imagery whether or not movements were executed.

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