

Cerebral Structures Participating in Motor Preparation in Humans: A Positron Emission Tomography Study

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SUMMARY AND CONCLUSIONS

1. Using positron emission tomography and measurement of regional cerebral blood flow (rCBF) as an index of cerebral activity, we investigated the central processing of motor preparation in 13 healthy volunteers.

2. We used a motor reaction time paradigm with visual cues as preparatory and response signals. A preparatory stimulus (PS) provided either full, partial, or no information regarding two variables of a forthcoming right finger movement: finger type (index or little finger) and movement direction (abduction or elevation). After a variable delay period, a response stimulus (RS) prompted the movement. A condition was also tested in which the subject could freely select any of the four possible movements during the preparation period ("free" condition). The timing of events was designed to emphasize the motor preparation phase over the motor execution component during the scanning time of 1 min.

3. Distinct preparatory processes, which depended on the information contained in the PS, were demonstrated by significant differences in reaction time between conditions. The reaction time was shorter in the "full" and free conditions, intermediate in the two partial information conditions ("finger" and "direction"), and longer when no preparatory information was available ("none" condition). Conversely, movement time and movement amplitude were similar between conditions, establishing the constancy of the motor executive output.

4. In comparison with a "rest" condition, which had matched visual inputs, the different conditions of motor preparation were associated with increased rCBF in a common set of cerebral regions: the contralateral frontal cortex (sensorimotor, premotor, cingulate, and supplementary motor cortex), the contralateral parietal association cortex (anterior and posterior regions), the ipsilateral cerebellum, the contralateral basal ganglia, and the thalamus. This observation substantiates the participation of those cerebral structures in the preparation for movement. Furthermore, the similarity of the activated areas among the different conditions compared with the rest condition suggests a single anatomic substrate for motor preparation, independent of the movement information context.

5. Differing amounts of movement information contained in the PS affected rCBF changes in some cerebral regions. In particular, the rCBF in the anterior parietal cortex (Brodmann's area 40) was significantly larger in each of the full, finger, and direction conditions, individually, compared with the none condition. This observation supports the hypothesis that the anterior parietal association cortex plays a major role in the use of visual instructions contained in the PS for partial or complete preparation to perform a motor act. On the other hand, the posterior parietal association cortex (Brodmann's area 7) was more activated in the finger, direction, and none conditions than in the full condition. This increased activity with restricted advance information suggests that the poste-

rior region of the parietal cortex is concerned with correct movement selection on the basis of enhanced spatial attention to the RS.

6. In contrast with the parietal cortex, the secondary motor areas (i.e., premotor cortex, cingulate cortex, and supplementary motor area) showed similar activity regardless of the degree of preparation allowed by the advance visual information. Thus the parietal cortex may play a more crucial role than the secondary motor areas in integrating visual information in preparation for movement.

7. The effect on brain activity of the internal (self-generated) versus the external (cued) mode of movement selection was assessed by comparing the free and full conditions, the preparatory component being matched in the two conditions. The anterior part of the supplementary motor area was the main area preferentially involved in the internal selection of movement, independently of motor preparation processes.

INTRODUCTION

Motor preparation was defined by Henry and Rogers (1960) as the act of "establishing a state of readiness to make a specific planned movement." This definition introduces two complementary notions, readiness and specificity, that probably coexist in the phase preceding the execution of a movement. The neuronal substrates of motor preparation have been extensively investigated in monkeys using the reaction time (RT) paradigm. This paradigm typically consists of a preparatory stimulus informing the animal about the movement, followed by a delay period during which the monkey must withhold the behavior, followed by a response stimulus signaling the initiation of the movement. Neuronal activity occurring during the delay period has been described in various cortical areas, mainly in the prefrontal cortex, the premotor cortex (PMC), the supplementary motor area (SMA), the primary motor cortex, and the parietal cortex (Crammond and Kalaska 1989; Fuster 1973; Riehle and Requin 1989; Tanji et al. 1980; Tanji and Evarts 1976; Weirich and Wise 1982). The activity during the delay period mainly reflects the preparation for specific motor actions in the PMC (Wise and Kurata 1989; Wise et al. 1992), and may also reflect motor preparation in other frontal cortical fields (see Wise 1989 for a review).

In humans, numerous regional cerebral blood flow (rCBF) studies in which positron emission tomography (PET) was used have been devoted to the cerebral motor system. Studies on motor processing include execution of simple and complex motor acts (Colebatch et al. 1991;

Grafton et al. 1991, 1992b, 1993; Matelli et al. 1993; Roland et al. 1980a,b; Sabatini et al. 1993; Shibasaki et al. 1993), imagination of movement (Decety et al. 1990; Fox et al. 1987; Roland et al. 1980a; Stephan et al. 1995), and motor learning (Grafton et al. 1992a; Jenkins et al. 1994; Seitz and Roland 1992; Seitz et al. 1990). In those reports, the issue of motor preparation has received little attention. The absence of rCBF data during motor preparation could be related to the limited temporal resolution of PET, which hampers the distinction between the preparation phase and the execution phase of a movement. Kawashima et al. (1994) addressed the question of preparation for reaching by limiting their scanning time to the delay period between visual target exposure and actual reaching. However, considering the duration of their preparation period (90 s), it is likely that processes other than motor preparation per se occurred, including visuospatial working memory or mental imagery. This stresses the fact that motor preparation can easily be confused with other covert behavioral processes that may occur before a movement.

The difficulty of controlling for preparatory processes is further illustrated in a PET study on motor selection (Deiber et al. 1991), which showed that the anterior SMA was more activated in tasks that were generated internally compared with tasks that were instructed by external cues. From this observation, the anterior SMA [now defined as pre-SMA (Matsuzaka et al. 1992)] could be interpreted as being specialized in the internal guiding of movements. However, the internally generated movements were associated with shorter RTs than the externally guided movements, suggesting different preparatory processes in the two types of tasks. Such a difference would be expected because in the internally generated tasks the subjects could plan movements beforehand, whereas in the externally cued tasks the subjects had to wait for the tones to select and prepare the appropriate movement. A question thus remained as to which process was responsible for the rCBF increase in the pre-SMA: the mode of movement selection (internal), or, alternatively, the degree or time of movement preparation.

Our aim in this study was to investigate the neuroanatomic correlates of motor preparation in humans. Processes of motor preparation were controlled by designing tasks that differed only in the preparatory phase before movements. The experimental design was derived from the movement precuing method, which manipulates information about the variables of a forthcoming movement (Rosenbaum 1983). A motor RT paradigm was used, in which information regarding the forthcoming movement was complete, partial, or absent. We also tested a condition in which the subjects were free to select any movement during the preparatory period. Visual cues were used for the preparatory signal (PS) and the response signal (RS). Special attention was paid to minimizing the execution-related processes with respect to the preparation-related processes in the 1-min scan time from which the rCBF images were derived. Preliminary results of this study have been reported previously (Deiber et al. 1994).

METHODS

Subjects

We studied 13 normal male volunteers aged 22–41 yr (mean 31 yr). All were right-handed as measured by the Edinburgh Inventory

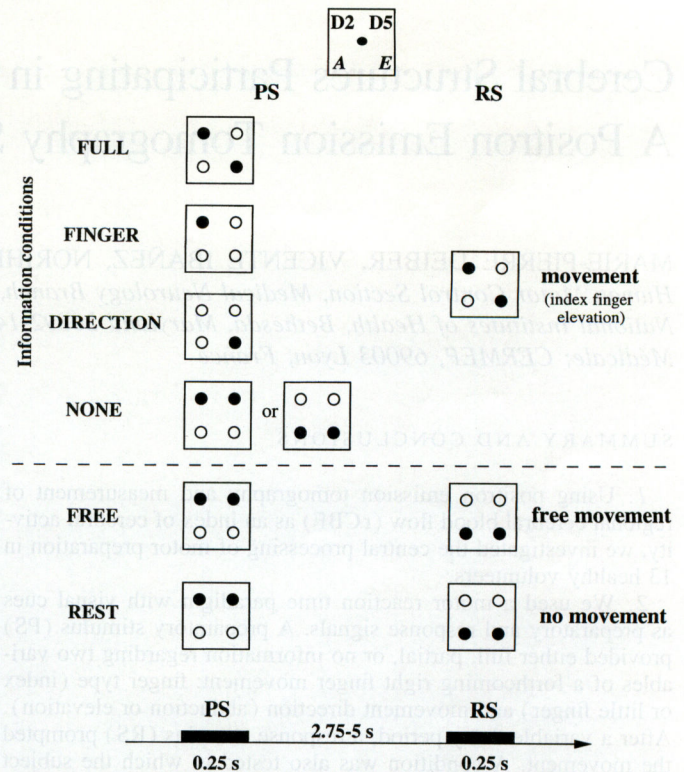


FIG. 1. Schematic diagram of the tasks. *Top square*: location of each light-emitting diode (LED) is replaced by the movement components (D2, index finger; D5, little finger; A, finger abduction; E, finger elevation). For clarity, the eye fixation point is only shown in the *top square*. PS, preparatory stimulus; RS, response stimulus. Filled circles: illuminated LEDs. The selected example, RS = D2 + E, requires elevation of the index finger, and the possible PSs are shown for each of the information conditions. In the free condition, the combination D2 + D5 represents the PS, which requires the subject to prepare the movement of his choice; the combination A + E represents the RS, which prompts the execution of the freely selected movement. In the rest condition, the subject is instructed not to move while the combinations D2 + D5 and A + E alternate.

(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 rCBF were performed sequentially using the tracer $H_2^{15}O$. During scanning the subjects made finger movements with the right hand, as brisk and large as possible. There were two movement variables: finger type (index finger or little finger) and movement direction (abduction or elevation). Therefore the following four movements were possible: index finger abduction, index finger elevation, little finger abduction, and little finger elevation. Finger type and movement direction were indicated by four light-emitting diodes (LEDs) arranged in a square and presented in the 10° of the central visual field, with a central gaze fixation point (Fig. 1). The upper two LEDs signified the finger type, with the upper left for index finger and the upper right for little finger. The lower two LEDs signified the movement direction, with the lower left for abduction and the lower right for elevation. A PS was presented for 250 ms, followed by a delay period varying from 2.75 to 5 s in intervals of 250 ms. During the delay period, the subjects were required to prepare movements according to the instruction presented by the PS. An RS was then

presented for 250 ms, prompting the subject to make the movement (Fig. 1). A total of 2.7 s elapsed after the RS before a new PS was presented. There were eight trials, and therefore eight movements in each 60-s scan.

An IBM PC computer was used to control the sequence of illumination of the different combinations of the LEDs and to monitor and store the behavioral data. The subjects' arm, wrist, and nonmoving fingers were fixed while the index finger or little finger movements were performed. Linear potentiometers coupled to each of the four movement axes provided a record of the finger displacements. The mechanograms were sampled with a frequency of 200 Hz, starting with the occurrence of the PS and ending 1,500 ms after the occurrence of the RS. RT, movement time (MT), and movement amplitude (MA) were calculated off-line using the stored mechanograms. The time between the occurrence of the RS and the deflection of the trace of the corresponding mechanogram was defined as RT; from the RT to the peak of the trace, the time elapsed was defined as MT and the corresponding amplitude as MA. The numbers of incorrect responses (i.e., incorrect finger or direction), as well as anticipated responses (movement starting before RS) and late responses (RT > 1,500 ms), were also recorded.

There were four "information" conditions, in which the RS always provided complete information about the movement (Fig. 1). The PS provided four types of information: 1) complete information (full condition), 2) information about which finger to move (finger condition), 3) information about movement direction (direction condition), and 4) no information—a meaningless combination of two LEDs (none condition). In addition, two conditions were tested in which neither RS nor PS provided any movement information: 1) subjects freely prepared one of the four possible movements during the delay period, randomizing the choice from trial to trial, with PS given by the two upper LEDs and RS by the two lower LEDs (free condition); and 2) subjects were at rest while the two upper and the two lower LEDs were alternately presented (rest condition).

In all conditions, including the rest condition, the subjects were asked to maintain the gaze on the central fixation point. The four information conditions were repeated twice, with the free and rest conditions consistently performed between the first and the second presentation of the information conditions: A B C D E F D C B A. The order of presentation of the information conditions (A, B, C, D) and of the free and rest conditions (E, F) was pseudorandomized between subjects. Different combinations of LEDs were presented in each repetition of the information conditions. To control for motor output, the sequences were made such that each of the four movements was required twice in the eight trials. The subjects were trained 1 day before the PET scan on each of the information conditions until reaching an overall criterion of 90% success on all tasks. The subjects also had one session of training on the free condition. The aim of the training was to make the subjects familiar with the tasks without overlearning.

Data acquisition

PET scanning was performed using a Scanditronix PC2048-15B tomograph (Uppsala, Sweden); resolution after reconstruction is $6.5 \times 6.5 \times 6.5$ mm (full width half-maximum). This tomograph allows simultaneous acquisition of 15 parallel transaxial planes of data separated by 6.5 mm (center to center), with a total axial field of view of 9.75 cm. Emission scans were acquired parallel to the orbitomeatal line, beginning between 20 and 30 mm above the orbitomeatal line, and were attenuation corrected with a transmission scan collected before each session during the exposure of a $^{68}\text{Ge}/^{68}\text{Ga}$ external rotating source. Head movements during the scans were minimized by using a thermoplastic mask that was

molded to each subject's head and attached to the scanner bed. 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, 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 reconstructed PET images contained 128×128 pixels, each 2×2 mm. The 15 original axial planes of each PET image (interplanar distance 6.5 mm) were interpolated linearly to 43 planes to produce approximately cubic voxels. Each rCBF image was reorientated to the intercommissural (AC-PC) line and re-scaled to fit the standard stereotaxic space of Talairach and Tournoux (1988). This resulted in 26 planes parallel to the AC-PC plane with a voxel size of $2 \times 2 \times 4$ mm (Friston et al. 1989). These slices were resampled in a nonlinear fashion to account for differences in brain shape (Friston et al. 1991a). Images were smoothed with a Gaussian kernel filter of $20 \times 20 \times 12$ mm to compensate for remaining intersubject gyral variability and to increase signal-to-noise ratio. Differences in global activity between subjects and conditions were removed by analysis of covariance with global cerebral blood flow as the confounding variable (Friston et al. 1990). This process resulted in the generation of a group mean activity for each task, adjusted to a single overall global cerebral blood flow of $50 \text{ ml} \cdot 100 \text{ ml}^{-1} \cdot \text{min}^{-1}$, with an associated residual error variance across subjects for each pixel. The pixel values of rCBF together with the associated adjusted error variances were used for further statistical analysis. Planned comparisons between conditions were performed using a two-tailed *t*-statistic corrected for multiple nonindependent comparisons and a threshold set at $P < 0.05$. The results were displayed as statistical parametric maps (SPMs) of significant focal changes in rCBF (Friston et al. 1991b).

Planned comparisons were made between conditions as follows: 1) comparisons of each individual condition (full, finger, direction, none, free) with the rest condition; 2) comparisons between information conditions (full, finger, direction, none), for a total of 12 comparisons; and 3) comparison between free and full conditions.

Designation of anatomic structures

As described above, the procedure used for group analysis of the PET data was based on the resizing of the PET scans to the standard anatomic space of the atlas of Talairach and Tournoux (1988). This procedure allowed us to report activated foci in terms of Talairach and Tournoux coordinates, with reference to Brodmann's areas (BAs) as identified in the atlas. This technique has obvious limitations of spatial resolution, and the designation of the anatomic structures is tentative rather than definitive, as it would be if obtained by experimental studies where exact localization is determined anatomically.

RESULTS

Task performance

Figure 2 shows the percentage of errors made by the subjects. The errors were subdivided into 1) movement errors,

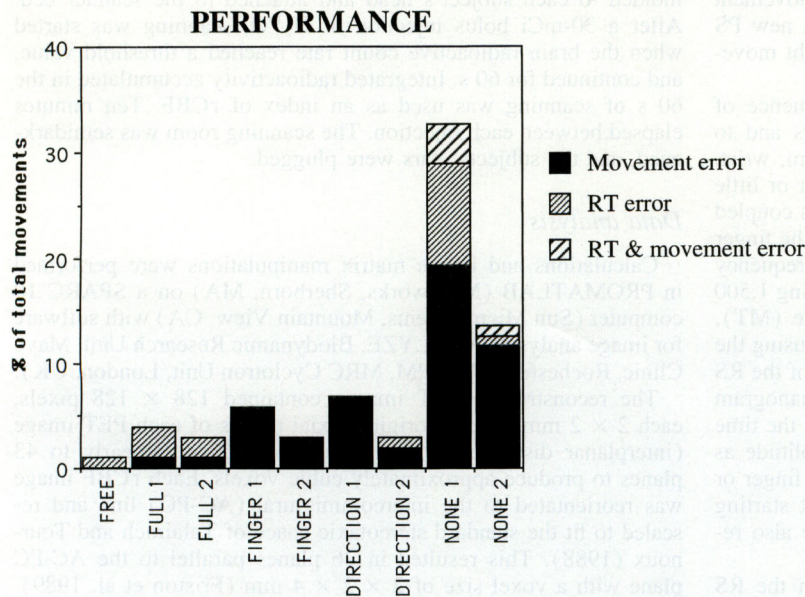


FIG. 2. Mean movement performance over the 13 subjects expressed in each condition as the number of errors in percentage of the total number of movements performed. Movement error: incorrect movement with respect to the RS; reaction time (RT) error: RT > 1,500 ms or RT < 0; RT & movement error: movement and RT errors combined.

defined as incorrect movements with respect to those requested by the visual cues, 2) RT errors, defined as values >1,500 ms as well as negative values (movements initiated before the RS); and 3) combined movement and RT errors. The number of movement errors was much larger than the number of RT errors or combined movement and RT errors. The subjects made more errors in the none condition irrespective of the type of error. In each condition, the second repetition contained fewer errors than the first. The improvement in performance suggested the occurrence of a learning effect between the two repetitions of the same condition, which would be expected because the tasks were not overlearned.

Figure 3 shows the intersubject means and standard deviations for the RT, MT, and MA. A three-factor analysis of variance was performed on each of these three measures to study the respective contribution of the condition, finger type, and movement direction. The RT was significantly affected by the condition ($F = 102.78$, $P < 0.0001$), but not by the finger type or the movement direction. A post hoc Scheffé test revealed significant RT differences between all conditions, except between repetitions of the same condition, between the free and full conditions, and between the finger and direction conditions. MT and MA were not affected by the condition, but were affected by the finger type (MT: $F = 12.13$, $P < 0.001$; MA: $F = 79.7$, $P < 0.0001$) and the movement direction (MT: $F = 51.2$, $P < 0.0001$; MA: $F = 4.71$, $P < 0.05$). A post hoc Scheffé test revealed that MT was significantly longer for little finger movements than for index finger movements, and for vertical movements (elevations) than for horizontal movements (abductions). With the same test, MA was significantly larger for index finger than for little finger movements, and for vertical movements than for horizontal movements.

Comparisons of individual conditions with rest

The RT did not differ between repetitions of the same task. However, because differences in performance were ob-

served, each condition was analyzed for differences in rCBF between the first and the second repetitions. Because the results did not show any significant rCBF differences, the same weight was given to the two repetitions of the same task for further analysis. Figure 4 shows the significant increases in rCBF for each of the information conditions, as well as for the free condition, with respect to the rest condition. The areas in which the rCBF was significantly increased are listed in Table 1.

The following structures were commonly activated in all the conditions: cerebellum, left striatum, left thalamus, left anterior parietal cortex (BA 40), left PMC, rostral cingulate cortex (BA 32), and SMA. However, in the majority of those areas the extent of activation differed according to the condition. The cerebellar activation was restricted in the free condition but extensive in the none condition. The opposite trend was seen in the PMC, SMA, and cingulate cortex, which were extensively activated in the free condition but restrictively in the none condition. In the SMA, the peak of activation was more anterior for the free condition ($y = +10$ mm; pre-SMA) than for the full condition ($y = -6$ mm), the finger condition ($y = +2$ mm), the direction condition ($y = 0$ mm), and the none condition ($y = 0$ mm), the coordinates for which are in the SMA proper.

Besides cerebral areas activated in all conditions, there were other structures in which rCBF increases were only significant in some conditions (see Table 1). Among those regions, the left sensorimotor cortex (SMC) was significantly activated in all conditions except in the none condition, and the left posterior parietal cortex (BA 7) was significantly activated in the finger, direction, and none conditions but not in the free and full conditions.

Comparisons between information conditions

To get a general idea of the intensity of activation according to the information condition, we plotted the mean normalized rCBF values for each information condition in

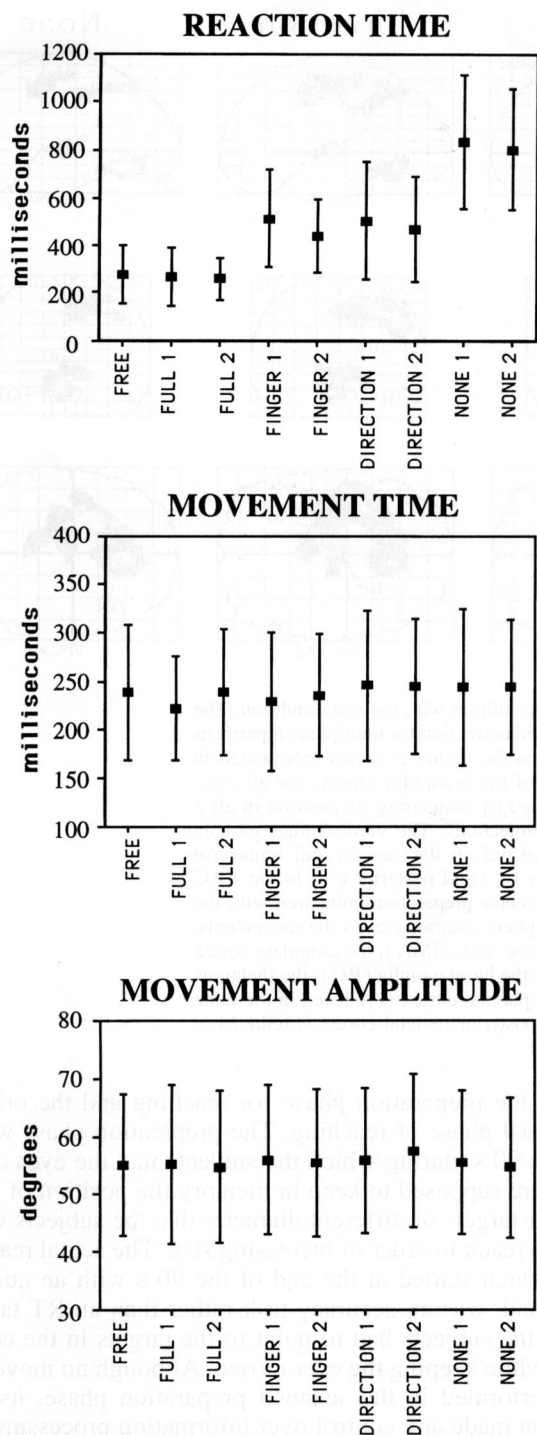


FIG. 3. Grand averages and standard deviations over the 13 subjects in each condition for RT, movement time, and movement amplitude. Only the RT was significantly affected by the condition (3-factor analysis of variance, see text for details).

the major cerebral structures highlighted by the comparisons with the rest condition (Fig. 5); the plots were obtained for each structure at the mean coordinates of peak activation between the four information conditions (see Table 1). The effect of precuing information on the rCBF values was assessed in each structure by a one-factor analysis of variance.

Three categories of areas were distinguished according to the rCBF pattern across the four information conditions: 1) areas where the rCBF tended to decrease with reduced information in the PS, 2) areas where the rCBF tended to increase with reduced information in the PS, and 3) areas without consistent changes relative to the information content of the PS. The SMC and anterior parietal area 40 belonged to the first group; the cerebellum and posterior parietal area 7 belonged to the second group; the PMC, cingulate cortex, and SMA proper belonged to the third group.

A pixel-by-pixel analysis of the differences between information conditions was then assessed by SPM. A few areas, listed in Table 2, showed significant changes. A consistent observation was a significant increase of activation in the left anterior parietal area 40 when each of the full, finger, and direction conditions were compared with the none condition. Moreover, the comparison of the finger condition with the full condition evidenced an activation of the left parietal area 7 close to the midline (Table 2).

Comparison of free and full conditions

Figure 6 shows that in comparison with the full condition, the free condition induced an rCBF increase in the prefrontal cortex (BA 10 on the left side and BA 9 bilaterally), the PMC (BA 8) bilaterally and medially, the rostral cingulate cortex (BA 32), the pre-SMA, and the left parietal cortex (BA 40). Table 3 lists those areas more active in the free than in the full condition. No significant decreases were evidenced (i.e., no area showed activity significantly greater in the full than in the free condition).

DISCUSSION

In the present study we used the RT paradigm to explore the cerebral processes underlying movement preparation. PET temporal resolution (60 s) is insufficient to focus on the rCBF pattern within the delay period, in which the preparatory processes are supposed to occur. To overcome this limitation, the paradigm was designed so that the subjects would spend much more time in preparation than in actual motor execution: within 1 min of scanning there were eight movements, each ~500 ms in duration, in contrast with an average of 3.9 s per trial spent in the delay period. Because of that proportion, we argue that the images obtained by integrating activity over 1 min of scanning mainly reflect neuronal activity related to preparatory rather than to executive processes. In support of this interpretation, MacKinnon et al. (1994) found that 2-Hz serial movements involved significant activation of the contralateral SMC and other cerebellothalamic structures, whereas intermittent movements at 0.2–0.08 Hz were mostly accompanied by activity in the SMA with minimal activation of the SMC. Dipole source analysis performed on electroencephalographic epochs recorded before electromyographic onset gave results concordant with the PET data. In our laboratory, Sadato et al. (1996) showed that auditory-cued, simple index-thumb opponent movements performed at slow rates (0.25 and 0.5 Hz) were not accompanied by any activity in the motor structures except in the SMA, whereas the same movements

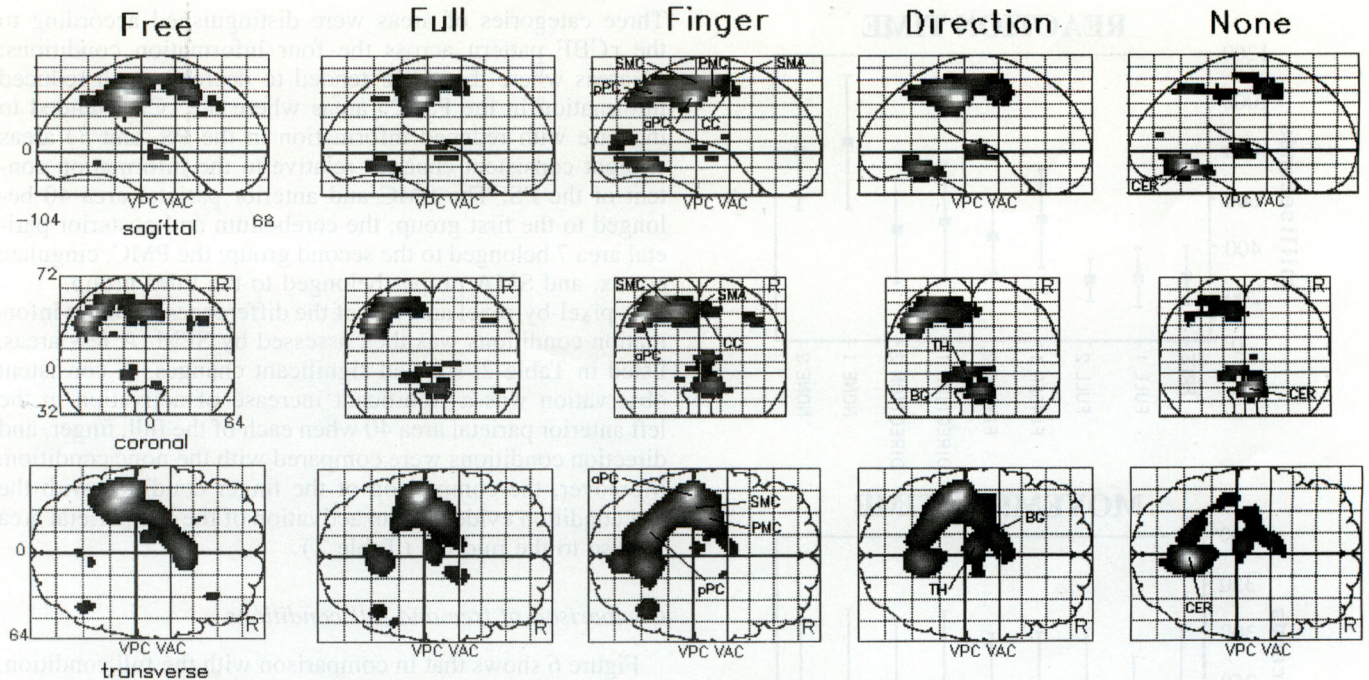


FIG. 4. Statistical parametric maps (SPMs) for the comparison of each individual condition with the rest condition. The pixels reflecting t -values exceeding the significance threshold of $P < 0.05$ after Bonferroni correction for multiple comparisons are displayed using a gray scale, with the lower Z scores represented in dark gray and the higher Z scores represented in light gray. Pixels are displayed on single sagittal, coronal, and transverse projections of the brain (for clarity, not all areas of activation are labeled). The spatial location of each activated area can be established by comparing its position in all 3 views. The intercommissural (AC-PC) line is set at 0 on the sagittal and coronal projections. The vertical lines passing through the anterior commissure (VAC) and posterior commissure (VPC) are depicted on the sagittal and transverse projections. Distances are in mm above (+) and below (-) the AC-PC line, anterior (+) and posterior (-) to the VAC line, and on the left (-) and right (+) of the midline. In the different conditions of motor preparation compared with the rest condition, the regional cerebral blood flow (rCBF) mainly increases in the hemisphere contralateral to the movements, in the sensorimotor cortex (SMC), the premotor cortex (PMC), the supplementary motor area (SMA), the cingulate cortex (CC), the parietal cortex (aPC, anterior parietal cortex; pPC, posterior parietal cortex), the basal ganglia (BG), the thalamus (TH), and the ipsilateral cerebellum (CER). Notice that 1) the activity in the anterior parietal cortex is reduced in the none condition compared with the other information conditions, and 2) the activity in the posterior parietal cortex is reduced in the full condition compared with the other conditions, particularly the finger condition.

performed at faster rates did activate the ipsilateral cerebellum and the contralateral SMC. These findings support the view that with the exception of the SMA, no rCBF increases were to be expected for the frequency range of movement used in the present study (0.13 Hz). This supports the evidence that the activity observed in the cerebral motor structures in the present RT tasks is due to preparatory processes rather than motor execution per se.

Theoretically, an ideal control condition would have been a task matching the executive component of the conditions but without motor preparation. However, such a task is not available because there are no absolute criteria to ascertain the absence of a preparatory process in a given motor task, even the most simple one. In the none condition, in which no specific movement can be planned in advance, the presence of a readiness to move cannot be ruled out. Indeed, motor readiness has been shown to occur identically in both simple (advance information) and choice (no advance information) RT tasks (Brown and Robbins 1991). This reinforces the notion that motor readiness could indeed be considered a nonspecific, obligatory component of motor preparation, which would be present in every motor task. Recently, Kawashima et al. (1994) scanned two groups of subjects,

one in the preparation phase for reaching and the other in the actual phase of reaching. The preparation phase was as long as 90 s, during which the subjects had the eyes closed and were supposed to keep in memory the position of seven circular targets of different diameter that the subjects would have to reach in order of increasing size. The actual reaching task, which started at the end of the 90 s with an auditory command, was an accuracy task rather than an RT task, in which the subjects had to point to the targets in the correct order while keeping the eyes closed. Although no movement was performed in the scanned preparation phase, its long duration made any control over information processing during this interval problematic. It is likely that processes other than motor preparation per se, such as visuospatial memory or mental imagery, had a strong influence during that time period. Moreover, the intersubject variability on the nature and timing of the cerebral processes was probably high.

Relations between rCBF and motor preparation

The present results reveal highly significant differences in RT that depend on the amount of information contained in the preparatory stimulus, thus providing evidence for the

TABLE 1. Comparisons of individual conditions with the rest condition

Area Activated	Extent of Area, mm	Talairach Coordinates			Z Score	Percent Change in Normalized rCBF
		x	y	z		
Full vs. rest						
Cerebellum	-16 to -4	6	-58	-8	5.2	4.0
Striatum (L)	-4 to +4	-18	-10	-4	4.3	3.9
Striatum (R)	+8	14	2	8	4.4	3.7
Thalamus (L)	0 to +8	-6	-16	8	3.8	3.5
Anterior area 40 (L)	+28 to +56	-44	-28	40	6.7	5.5
Posterior area 40 (R)	+40	40	-56	40	4.0	4.5
SMC (L)	+40 to +56	-32	-22	52	5.5	4.5
PMC (L)	+52 to +56	-30	-16	56	6.2	5.9
Area 32	+44	-10	2	44	4.0	3.3
SMA	+48 to +52	-16	-6	52	4.4	3.8
Finger vs. rest						
Cerebellum	-16 to 0	8	-60	-8	5.7	4.5
Striatum (L)	-4	-14	-12	-4	3.9	4.0
Thalamus (L)	+4	-6	-22	4	4.1	3.8
Thalamus (R)	+12	12	-2	12	3.8	4.7
Area 17/18	0 to +16	6	-78	12	5.1	3.7
Anterior area 40 (L)	+32 to +56	-44	-26	40	6.4	5.0
Posterior area 40 (R)	+36 to +44	40	-58	40	4.5	5.3
Area 7 (L)	+40 to +56	-18	-56	44	5.9	4.5
SMC (L)	+40 to +56	-36	-26	48	5.5	4.3
PMC (L)	+52 to +56	-28	-14	56	6.0	5.7
Area 32	+44	-8	2	44	4.0	3.0
SMA	+48 to +52	-8	2	48	4.2	3.4
Direction vs. rest						
Cerebellum	-20 to -4	6	-56	-12	5.8	5.8
Striatum (L)	-4 to 0	-14	-12	-4	4.7	5.0
Thalamus (L)	0 to +8	-4	-16	4	5.3	4.7
Thalamus (R)	+4	14	-16	4	4.0	3.9
Anterior area 40 (L)	+28 to +56	-44	-28	40	6.4	5.4
Area 7 (L)	+40 to +52	-30	-40	48	5.7	4.7
SMC (L)	+40 to +56	-36	-26	48	5.3	4.4
PMC (L)	+44 to +56	-28	-16	56	5.2	4.9
Area 32	+36 to +44	-12	-2	44	5.0	4.5
SMA	+48 to +56	-10	0	48	4.8	4.4
None vs. rest						
Cerebellum	-20 to 0	4	-58	-12	6.1	6.8
Striatum (L)	-4 to 0	-14	-16	-4	4.5	5.3
Thalamus (L)	0 to +4	-6	-20	4	4.9	5.1
Area 17/18	+12	6	-78	12	3.9	3.1
Anterior area 40 (L)	+36 to +44	-42	-30	40	4.0	3.7
Area 7 (L)	+44 to +48	-18	-56	44	4.6	4.0
PMC (L)	+52 to +56	-28	-14	56	4.3	4.6
Area 32	+40 to +44	-4	10	44	4.1	3.6
SMA	+48 to +52	-10	0	48	4.7	4.7
Free vs. rest						
Cerebellum	-8	8	-56	-8	3.9	3.4
Striatum (L)	-4 to 0	-14	-10	-4	4.3	4.6
Thalamus (L)	0 to +4	-10	-16	4	3.8	4.5
Anterior area 40 (L)	+24 to +56	-44	-32	40	6.1	5.6
Posterior area 40 (R)	+36 to +40	42	-62	40	4.1	6.0
SMC (L)	+40 to +56	-32	-20	52	4.8	4.5
PMC (L)	+52 to +56	-28	-12	56	5.0	5.1
Area 32	+36 to +44	0	12	44	5.3	4.4
SMA	+48 to +56	-2	10	48	5.1	4.2
Area 9 (L)	+28	-26	22	28	3.8	4.0
Area 9 (R)	+32 to +40	32	32	36	4.0	4.0

Extent of area activated relative to intercommissural (AC-PC) line. Talairach coordinates and Z score of peak activation. rCBF, regional cerebral blood flow; L, left hemisphere; R, right hemisphere; SMC, sensorimotor cortex; PMC, premotor cortex; SMA, supplementary motor area.

occurrence of distinct preparatory processes. The various RT tasks were accompanied by increases in rCBF in common cortical and subcortical areas: SMC, PMC, SMA, cingulate cortex, parietal cortex, basal ganglia, thalamus, and cerebel-

lum. One main observation from the present study is that the dramatic changes in RT between conditions, which reveal a strong dependency of the preparation process on the precuing information, were not paralleled by distinct cerebral rCBF

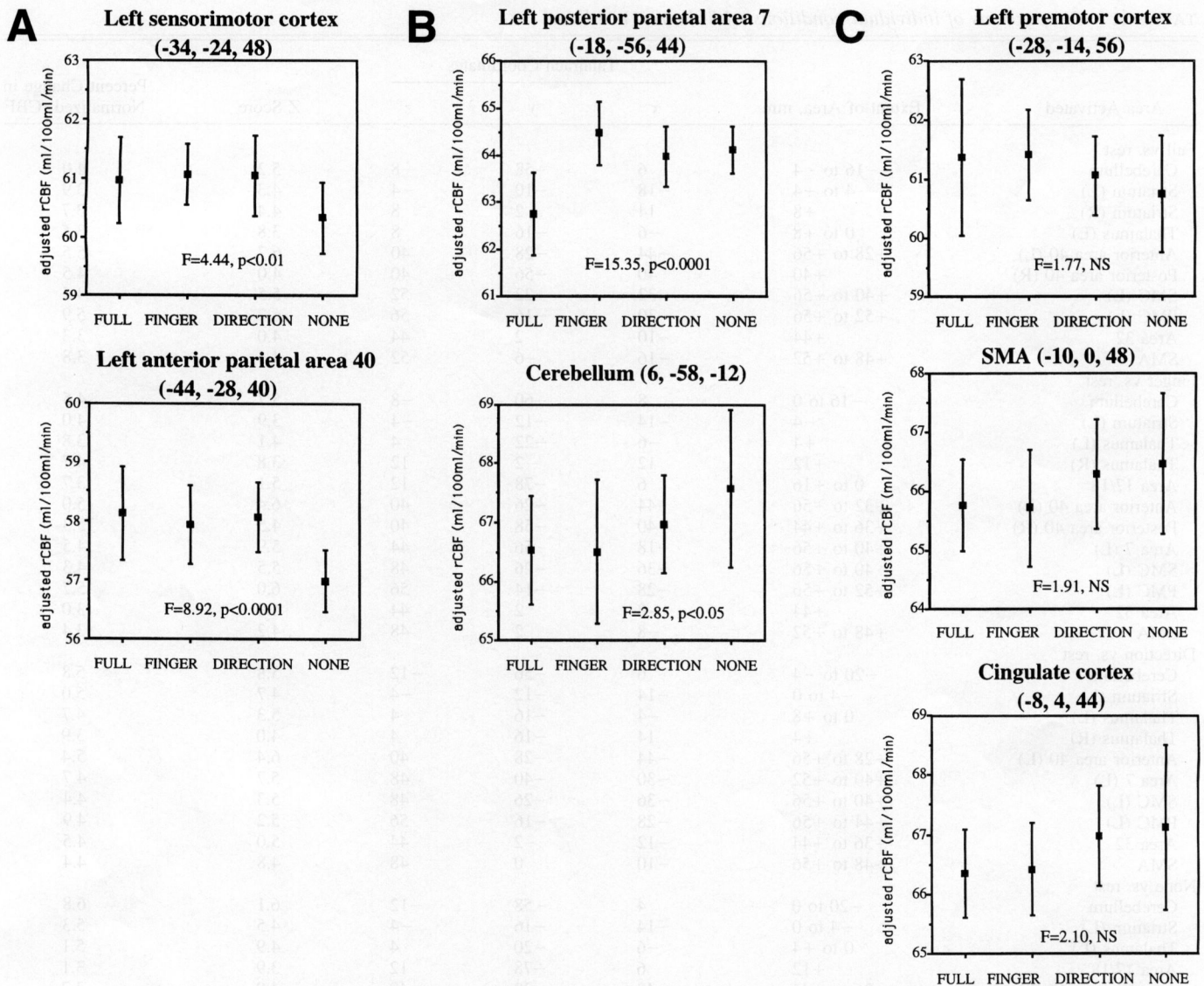


FIG. 5. Grand averages and standard deviations of the analysis-of-covariance-adjusted rCBF over the 13 subjects in each information condition in the major cerebral structures identified by comparisons with the rest condition. Plotting coordinates (x, y, z) of the cerebral regions correspond to the mean coordinates of peak activation over the four information conditions individually compared with the rest condition. A 1-factor analysis of variance was performed to assess the effect of advance information on rCBF values. The F and P values are given for each plot. A: rCBF decreased with absence of advance information. B: rCBF increased with absence of advance information. C: no significant change in rCBF with advance information.

patterns. With the exception of two restricted regions in the anterior and posterior parietal association cortex, which will be discussed later, the rCBF patterns between each information condition were not significantly different on a pixel-by-pixel basis, as assessed by SPM. One could invoke a lack of sensitivity, an insufficient number of subjects, or inadequate scan repetition to explain this finding. However, lowering the threshold of significance did not change the results: no specific area showed rCBF changes in relation to a particular information condition. The similar pattern of cerebral activation in the four information conditions thus suggests that preparation to move results from the activity of a distributed cerebral network rather than the activity of discrete cerebral regions that would "turn on" or "turn off" ac-

ording to the information context. However, although the number and pattern of cortical areas activated during motor preparation did not markedly vary, instructional information could have a differential effect on the level of rCBF changes. Below, each cerebral region is discussed in relation to its possible role in motor preparation, with consideration of the rCBF changes with differential instructional information.

Motor cortical fields: SMC, PMC, SMA

Neuronal activity in the three main cortical motor fields, namely, SMC, PMC, and SMA, has been extensively investigated in monkeys with the use of RT paradigms. These paradigms include "set-related" or "preparatory" activity,

Free vs Full

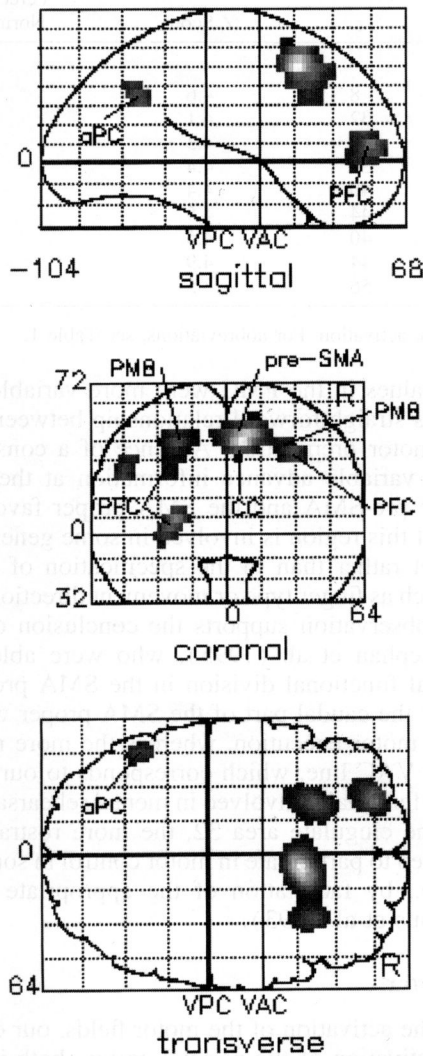


FIG. 6. SPMs for the comparison of the free condition with the full condition. Same conventions as in Fig. 4. With respect to the full condition, the rCBF is increased in the free condition in the anterior SMA (pre-SMA), the CC, premotor area 8 (PM8), bilateral prefrontal area 9 and left prefrontal area 10 (PFC), and the left aPC.

which starts after the preparatory stimulus and lasts until the beginning of the movement, and "movement-related" or "execution-related" activity, which typically precedes movement onset and is time-locked with it (Fuster 1973;

Riehle and Requin 1989; Tanji and Evarts 1976; Tanji et al. 1980; Weinrich and Wise 1982). Although these patterns are all present in SMC, PMC, and SMA, their relative proportion differs in each area: the SMC contains the largest proportion of movement-related neurons, whereas there are proportionally more set-related neurons in PMC and SMA (Alexander and Crutcher 1990; Halsband et al. 1994; Kurata and Wise 1988; Mushiake et al. 1991; Okano and Tanji 1987; Requin et al. 1990; Riehle and Requin 1989; Weinrich et al. 1984). Our rCBF results support the hypothesis that the SMC, PMC, and SMA participate in preparation for movement, but do not provide any evidence for preferential activation of PMC and SMA over SMC. One possible reason for this observation could be that the proportional difference between execution- and preparation-related cells reported between the motor fields is not large enough to be reflected at the macroscopic level of rCBF changes. PET studies dealing with cerebral activity during preparation for reaching have brought contradictory results. In a preliminary report on eight subjects, Decety et al. (1992) failed to find any activation in the motor fields; when two subjects were added to the data set and a more sophisticated analysis was used, the same laboratory (Kawashima et al. 1994) reported increased rCBF in SMC, SMA, and PMC.

The activity in PMC was strongly lateralized to the left hemisphere (contralateral to movements). Single-unit recordings have shown that a majority of the SMC neurons exhibited a contralateral relationship to movement, but that the relation between movement-related activity and the laterality of hand movements was more complex in PMC and SMA (Tanji et al. 1988). These authors suggested that the relation of the secondary motor area activity to movement was context dependent, being mainly contralateral in association with simple limb movements and more largely bilateral in association with complex motor actions. Such an observation was confirmed by several PET studies that showed a strong contralateral predominance of PMC activity in relation to simple finger movements (Colebatch et al. 1991; Kawashima et al. 1994; Shibasaki et al. 1993).

Among reports of set-related activity in the motor fields, several studies have indicated a rostral predominance for this type of response in SMC and SMA, showing a significant tendency for preparatory activity to be located more rostrally than movement-related activity (Alexander and Crutcher 1990; Matsuzaka et al. 1992; Weinrich et al. 1984). This observation is in accordance with data describing anatomic-functional subdivision within the SMA: the caudal part, or SMA proper, connected to the motor cortex and having direct

TABLE 2. Comparisons between information conditions

Conditions	Area Activated	Extent of Area, mm	Talairach Coordinates			Z Score	Percent Change in Normalized CBF
			x	y	z		
Full vs. none	Area 40 (L)	+36	-52	-24	36	3.6	2.9
Finger vs. none	Area 40 (L)	+36	-54	-20	36	3.9	2.9
Direction vs. none	Area 40 (L)	+24 to +36	-54	-22	32	4.3	3.0
Finger vs. full	Area 7 (L)	+44 to +52	-18	-58	44	4.6	3.0

Extent of area activated relative to AC-PC line. Talairach coordinates and Z score of peak activation. For abbreviations, see Table 1.

TABLE 3. Comparison between free and full conditions

Area Activated	Extent of Area, mm	Talairach Coordinates			Z Score	Percent Change in Normalized rCBF
		x	y	z		
Free vs. full						
Area 10 (L)	-4 to +12	-24	52	8	4.6	4.7
Area 9 (L)	+32 to +36	-28	24	32	4.1	3.4
Area 9 (R)	+36	30	22	36	4.3	3.6
Area 40 (L)	+32 to +36	-48	-56	32	4.4	3.6
Area 32	+36 to +40	4	20	40	4.4	3.1
Area 8 (L)	+40 to +48	-24	26	44	4.5	4.2
Area 8 (R)	+40 to +52	30	26	40	4.5	3.2
Area 8 (Medial)	+44 to +56	6	20	44	4.9	3.4
pre-SMA	+48 to +56	12	14	56	3.5	2.4

Extent of area activated relative to AC-PC line. Talairach coordinates and Z score of peak activation. For abbreviations, see Table 1.

connections to the spinal cord, is mostly active in relation to movement execution; the rostral part, or pre-SMA, connected to the prefrontal cortex and without projection to the spinal cord, is thought to be especially involved in higher-order motor control (Deiber et al. 1991; Dum and Strick 1991; Halsband et al. 1994; Luppino et al. 1993; Matelli et al. 1993; Matsuzaka et al. 1992). In the Talairach space for the human brain (Talairach and Tournoux 1988), the anatomic boundary between the pre-SMA and the SMA proper appears to correspond to the VAC line, which is the vertical line passing through the anterior commissure and perpendicular to the AC-PC line (see Passingham 1993 for a review). In our data, the SMA activation essentially occurred at the boundary between the pre-SMA and the SMA proper, except in the full condition, where it was more posterior, and in the free condition, where it was clearly anterior to the VAC line (Table 1). The averaged anteroposterior coordinate of the SMA between the four information conditions corresponded to the VAC line (0 mm).

Differential involvement of the motor fields in preparation for movement was suggested by their respective rCBF values across information conditions (Fig. 5): the SMC showed a tendency to be more active when some precuing information was present (full, finger, direction) than when it was absent (none); the PMC and the SMA did not show any consistent tendency. The fact that the motor output was kept constant between information conditions (Fig. 3) further supports the argument that variations in the preparation process were responsible for the tendency observed in the SMC. Riehle and Requin (1989, 1993) have recorded SMC and PMC neurons in monkeys in a paradigm similar to the one used in the present study. As in our study, RT decreased with an increasing amount of advance information. A correlational analysis between RT and discharge frequency during the delay period revealed similar correlation distributions for SMC and PMC neurons. Furthermore, an increase of discharge frequency during the delay period correlated with a shorter RT, and inversely, a decreased discharge frequency during the delay period correlated with a longer RT (Riehle and Requin 1993). Our own data are in agreement with those of Riehle and Requin concerning the SMC, suggesting its preferential implication when precuing information allowed some degree of specific preparation of the movement.

Although showing a similar tendency to those of the SMC,

the rCBF values in the PMC were more variable and suggested a less straightforward relationship between PMC activity and motor preparation. Absence of a consistent tendency with variable advance information at the boundary between the pre-SMA and the SMA proper favors the hypothesis that this region is involved in some general process of motor set rather than in the specification of movement variables such as finger type or movement direction. Interestingly, this observation supports the conclusion of a recent work by Stephan et al. (1995), who were able to make an additional functional division in the SMA proper. They showed that the caudal part of the SMA proper was mainly involved in motor execution, whereas the more rostral part close to the VAC line, which corresponds to our activation site, was preferentially involved in mental rehearsal of movements. In the cingulate area 32, the more rostral part was also suggested to participate in motor control in some general manner (i.e., by facilitation of the appropriate motor response) (Paus et al. 1993).

Parietal cortex

Besides the activation of the motor fields, our data reveal a marked activation of the parietal cortex, both in its more anterior part, identified as BA 40, and its posterior part, identified as BA 7.

ANTERIOR PARIETAL CORTEX. The anterior parietal region activated in the present study is designated as a single area by Brodmann (area 40) but involves portions of both inferior and superior parietal lobules. In the monkey, preparatory motor activity in relation to visual cues has been recorded in the rostralateral part of the inferior parietal lobule (BA 7b) (Godschalk and Lemon 1989), in the posterior parietal cortex near the intraparietal sulcus (Requin et al. 1990), and in BA 5 situated anteriorly in the superior parietal lobule (Crammond and Kalaska 1989). Although there remains some doubt about the exact location of the parietal neurons with preparatory-related activity, a common feature seems to be their rather anterior position within the parietal lobe. Decety et al. (1992) reported the activation of the angular (BA 39) and supramarginal (BA 40) gyri in the preparation phase for reaching. Our experiment shows that in the human brain the anterior part of the parietal cortex, tentatively designated as BA 40, is active during preparation for movement.

Moreover, when the SPM conservative statistical approach is used, this region of the brain is the only one to remain significantly more active in the three conditions in which relevant information was provided in the PS (full, finger, direction) compared with the none condition, in which the PS did not carry any specific information (Table 2). This finding supports a primary role of the anterior parietal association cortex in using visual information for specific motor preparation in humans. Furthermore, our data suggest that the localization of this functional attribute is restricted to the very anterior part of the parietal area 40 close to the postcentral gyrus.

The use of visual information for motor preparation primarily requires visual attention. In a recent work on visuospatial attention, Corbetta et al. (1993) described the activation of the superior parietal lobule around the postcentral sulcus when 15° peripheral locations of the visual field were selected on the basis of cognitive or sensory cues, independently of the execution of a motor response. The authors also reported activation in the PMC contralateral to the movements, which was linked to the execution of a motor response to detect stimuli. They concluded that parietal and frontal regions were related to different aspects of spatial selection, with parietal cortex engaged in the "perceptual" component and the frontal cortex in the "premotor" component. Although its center coordinates were slightly lower and more lateral, our anterior parietal cortex activation included the superior parietal cortex, as described by Corbetta et al. (1993). Our tasks bear similarity with Corbetta's in that the subjects were required to fixate the eyes on the central point of the panel while attending to peripheral LEDs located within 10° of the central visual field. It is therefore likely that a peripheral shift of attention similar to the one described by Corbetta and colleagues occurred in our tasks, and thus contributed to the parietal as well as premotor activation observed.

POSTERIOR PARIETAL CORTEX. The posterior parietal cortex activated in the present study lies in the superior parietal lobule and is tentatively designated as BA 7. Our data show a significant activation of the posterior parietal cortex in all conditions except in the full condition. The absence of posterior parietal activation in the full condition is statistically significant when compared with the finger condition (Table 2). Thus, unlike in the anterior parietal cortex, there was less activation in the posterior parietal cortex when full information about movement was provided; this observation was also illustrated in the rCBF values across tasks (Fig. 5). There are several lines of evidence suggesting that the posterior region of the parietal cortex is concerned with multimodal integration of external information, and thus provides a sensory representation of extrapersonal space (see Mesulam 1990 for a review). Involvement of the posterior parietal cortex in movement preparation has been suggested by a recent study showing reduced movement-related potentials in patients with lesions affecting this region of the brain (Singh and Knight 1993). Deiber et al. (1991) showed that the activation of the posterior parietal association cortex was consistently associated with motor selection processes in tasks requiring joystick displacements in different directions

with an auditory cue as a trigger for action. Grafton et al. (1992b) described the activation of bilateral superior parietal and precuneate cortex during visually guided tracking movements, and suggested the role of those parietal regions for integrating visual cues into movement selection. Thus, the involvement of the posterior parietal cortex in motor selection was suggested by two independent studies using distinct modes of sensory cues. Another common feature of those two studies was the spatial aspect of the task: moving a joystick in four possible directions (Deiber et al. 1991), and tracking a target moving on a screen (Grafton et al. 1992b). The latter study additionally showed that the posterior parietal cortex responded to an increment of the spatial complexity of the task. Our present study features a double spatial aspect, both in the sensory input (spatially coded LEDs) and in the motor output (moving the appropriate finger in the appropriate direction). As a consequence of restricting advance information about movement, there was a larger choice of motor outputs and more need for attention to the spatial attributes of the visual cues in the RS. The increasing rCBF in the posterior parietal cortex accompanying the reduction of advance information suggests that this cerebral region is involved in the correct selection of movement on the basis of spatial attention needed for decoding the RS.

Basal ganglia and thalamus

The motor circuitry of the basal ganglia comprises reentrant pathways that originate in various cortical areas and pass through the basal ganglia before returning to the frontal lobe, by way of specific portions of the thalamus (see Alexander 1994 for a review). Although the anatomy and physiology of the basal ganglia are known in some detail, their functions in the generation and control of movements remain poorly understood. In the putamen, a subpopulation of neurons showing movement-related activity contingent on the triggering of the movement by a sensory stimulus has been suggested to participate in sensorimotor associations (Kimura 1986). Alexander and Crutcher (1990), studying preparatory activity in parallel in the SMC, SMA, and putamen, have reported that the proportion of set-related neurons in the putamen was similar to that in the SMC, but smaller than that in the SMA. They also showed that, on average, the preparatory activity started later in the putamen than in the SMC and SMA, suggesting that some of the preparatory activity in the putamen may arise from corticostriatal inputs to this nucleus from SMC or SMA. Our data implicate the basal ganglia and thalamus in the processes by which movements are prepared in humans.

Cerebellum

Functional imaging in humans has brought contradictory data on the involvement of the cerebellum in motor programming. In tasks where the subjects were asked to imagine movements without executing them, Roland et al. (1980a), Fox et al. (1987), and Stephan et al. (1995), using imagination of simple distal movements, failed to show any activation of the cerebellum, unlike Decety et al. (1990), who used imagination of actions appropriate to tennis. Our own

data showing activation of the cerebellum in the various RT tasks suggest that there is preparatory activity for movement taking place in the cerebellum.

There was a tendency for increased rCBF in the cerebellum when advance information was reduced (Fig. 5). The restricted field of view did not allow us to sample the entire cerebellum; the activation involved the dorsal portion of the cerebellar nuclei ipsilateral to the movements and the cerebellar vermis. Cerebellar nuclei, ventrolateral thalamic nucleus, and motor cortex have been shown to change their activity before movement onset (Chapman et al. 1986; Schmied et al. 1979; Thach 1978). Recently, cooling of the dentate nucleus ipsilateral to the moving hand has been shown to increase the RT of the movements and to decrease the size of a field potential within the motor cortex contralateral to movements, which is thought to be of cerebellar origin (Tsujimoto et al. 1993). These data suggest that the initial motor command for RT tasks in the motor cortex is supported through the cerebellothalamocortical pathway. In such a view, the higher cerebellar activity in the none condition could be explained by a greater emphasis on cerebellar mechanisms to ensure a rapid activation of the motor circuitry in the absence of specific preparation. In other words, the cerebellum could be viewed as a key structure in the process by which the subject gets ready to move in a general sense; it would play a less important role when an action can be prepared in advance of the triggering event. This hypothesis is supported by findings in patients with cerebellar atrophy (Wessel et al. 1994): the peak amplitudes of the late movement-related cortical potentials were found to be significantly reduced in the patients compared with normal subjects, and the authors concluded that "a strong input from the cerebellum seems to be crucial for the generation of a normal motor potential close to movement onset." Our own data suggest that the cerebellum becomes more activated when immediate translation of a sensory command into a motor response is needed.

Internal motor selection: free condition versus full condition

Compared with the rest condition, the free condition activated essentially the same pool of cerebral areas activated by the four information conditions (Fig. 4). The only differences observed were the very restrictive activation of the cerebellum, the more anterior activation of the SMA and cingulate cortex, and the exclusive activation of the prefrontal cortex bilaterally (probably BA 9). According to Deiber et al. (1991), the pre-SMA, cingulate cortex, and prefrontal area 9 are regions crucially involved in motor selection. The internal motor selection process occurring during the free condition could be isolated in our study by comparing the free and the full conditions. In both conditions, the subjects knew what to do in advance, and the only difference was that in the free condition they knew it on the basis of an internal choice, whereas in the full condition they were instructed by the visual display. Because the motor action timing was matched between the two conditions, the motor preparation component could be considered similar in both conditions, as confirmed by similar RTs. Thus the main difference between the two tasks was the mode of motor selection.

In 1991, Deiber et al. contrasted tasks based on internal selection of movements with tasks in which movements were driven by external cues, and showed that internal motor selection was mainly associated with the activation of the pre-SMA, whereas externally driven motor selection was not accompanied by any significant cerebral activation. The design of the tasks was such that the preparation component between internally and externally cued tasks was not matched, as reflected by significant differences in RT, therefore introducing a potential confounding effect. By failing to show any significant decrease of activation in the free condition compared with the full condition, the present study confirms that the externally cued selection process is rather poor at activating the brain, in contrast with the internally generated process; in particular, this does not support a predominant role of the PMC in selection of movements based on external cues, as proposed by Passingham (1993). On the other hand, internal selection of movement, as assessed by significant rCBF increases in the free condition compared with the full condition, was associated with the activation of the pre-SMA, anterior cingulate cortex, left anterior parietal cortex, and various frontal areas bilaterally. Thus the present data support the evidence that self selection of movement is indeed a primary role of the pre-SMA, and also suggest that the internal selection process involves a distributed network of areas located mainly in the frontal lobe. This observation accords with a study showing that willed actions are essentially associated with increased blood flow in the prefrontal cortex (Frith et al. 1991). Previous data have also reported the crucial role of the anterior cingulate cortex in the attention to the selection for action, independently of the nature of the task (Frith et al. 1991; Pardo et al. 1990; Posner and Petersen 1990). Among the other frontal areas activated in relation to internal motor selection, the premotor area tentatively identified as BA 8 is mainly known to contain a region involved with control of eye movements (frontal eye fields; Bruce and Goldberg 1985; Bruce et al. 1985). However, previous data on the activation of this region in response to voluntary saccades in humans have reported a more posterior location of the frontal eye field than in the present study, namely one in the precentral gyrus (Fox et al. 1985; Petit et al. 1993). In the absence of eye movement recording during PET scanning, it cannot be ruled out that a larger number of eye movements occurred in the free condition than in the full condition. However, because the location of the activation does not match with the frontal eye field location in humans, our data suggest the involvement of premotor area 8 in internally driven motor selection rather than in generation of eye movements.

However, the potential effect of working memory has to be raised in the interpretation of the data. Indeed, in the free condition the subjects had to remember the previous movement to be able to randomize their actions; this remembrance of past events, which refers to episodic memory, was not required in the full condition. Encoding of novel information into episodic memory has been shown to activate the left frontal cortex, whereas retrieval of information from episodic memory has been related to activation of the right frontal cortex, left anterior cingulate sulcus, and bilateral parietal cortex (Kapur et al. 1994; Shallice et al. 1994;

Tulving et al. 1994a,b). It is thus possible that the activation observed in the frontal areas, anterior cingulate cortex, and left anterior parietal cortex in the free condition is related in some way to the encoding/retrieval processes in episodic memory of the previous movement performed. A recent study by Tanji and Shima (1994) has shown the involvement of the SMA proper in memory processes related to the order of forthcoming multiple movements, but to our knowledge there have been no studies on the involvement of the pre-SMA in such processes. Thus, unlike the other regions, the pre-SMA activation observed in the free condition is likely to be specifically related to the internal selection of movement.

Conclusions

The present study shows the cerebral structures involved in the process by which simple movements are prepared. As a whole, these structures correspond to those that have been shown to increase their activity in relation to the execution of simple motor acts, suggesting a tight coupling between processes of motor preparation and motor execution in terms of functional anatomy. Thus this observation does not support a strict dichotomy between regions of the brain preparing movement and those executing it. By the use of an RT paradigm, in our experiment we attempted to restrict the motor preparation component to a well-defined temporal process with relative constancy during the rCBF measurement. A major finding is the preponderant activation of the parietal association cortex in preparation of movements, with an opposite behavior of the anterior and posterior regions. The anterior parietal cortex was essentially active in association with specific preparation of movement on the basis of relevant visual information. On the other hand, the posterior parietal cortex was more active in the case of nonunique solutions for movement, as if this region were concerned with a representation of all the possible motor choices. In contrast with the parietal association cortex, the secondary motor fields (PMC, SMA, and cingulate cortex) were not affected by the amount of preparation. In support of these observations, electrophysiological recordings of the contingent negative variation with the use of a paradigm similar to ours have suggested that the nature of advance information does not affect the SMA, but affects the parietal lobe, as shown by varying amplitude of the contingent negative variation in the parietal region (Bonnet and MacKay 1989; MacKay and Bonnet 1990). Further investigation of the temporal pattern of those preparation processes using multi-channel recording would be useful to complement the present anatomofunctional data.

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