Functional Properties of Brain Areas Associated With Motor Execution and Imagery

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Hanakawa, Takashi, Ilka Immisch, Keiichiro Toma, Michael A. Dimyan, Peter van Gelderen, and Mark Hallett. Functional properties of brain areas associated with motor exectution and imagery. *J Neurophysiol* 89: 989–1002, 2003; 10.1152/jn.00132.2002. Imagining motor acts is a cognitive task that engages parts of the executive motor system. While motor imagery has been intensively studied using neuroimaging techniques, most studies lack behavioral observations. Here, we used functional MRI to compare the functional neuroanatomy of motor execution and imagery using a task that objectively assesses imagery performance. With surface electromyographic monitoring within a scanner, 10 healthy subjects performed sequential finger-tapping movements according to visually presented number stimuli in either a movement or an imagery mode of performance. We also examined effects of varied and fixed stimulus types that differ in stimulus dependency of the task. Statistical parametric mapping revealed movement-predominant activity, imagery-predominant activity, and activity common to both movement and imagery modes of performance (movement-and-imagery activity). The movement-predominant activity included the primary sensory and motor areas, parietal operculum, and anterior cerebellum that had little imagery-related activity ($-0.1 \sim 0.1\%$), and the caudal premotor areas and area 5 that had mild-to-moderate imagery-related activity ($0.2 \sim 0.7\%$). Many frontoparietal areas and posterior cerebellum demonstrated movement-and-imagery activity. Imagery-predominant areas included the precentral sulcus at the level of middle frontal gyrus and the posterior superior parietal cortex/precuneus. Moreover, activity of the superior precentral sulcus and intraparietal sulcus areas, predominantly on the left, was associated with accuracy of the imagery task performance. Activity of the inferior precentral sulcus (area 6/44) showed stimulus-type effect particularly for the imagery mode. A time-course analysis of activity suggested a functional gradient, which was characterized by a more "executive" or more "imaginative" property in many areas related to movement and/or imagery. The results from the present study provide new insights into the functional neuroanatomy of motor imagery, including the effects of imagery performance and stimulus-dependency on brain activity.

INTRODUCTION

Motor imagery has been extensively studied with PET and functional MRI (fMRI) techniques. Converging evidence indicates that motor imagery shares neural substrates with those underlying motor execution. However, less certain are how and to what extent neural substrates are shared between the two modes of motor-related behavior. For example, there has been some controversy in the neuroimaging literature regarding involvement of the primary motor cortex (M1) during motor imagery. Region-of-interest analyses from fMRI experiments often reveal mild activity increases in M1 during motor imagery (Lotze et al. 1999; Porro et al. 1996, 2000; Roth et al. 1996), while group averaged analyses from fMRI and PET do not (Deiber et al. 1998; Gerardin et al. 2000; Parsons et al. 1995; Stephan et al. 1995). Regrettably, many of those fMRI studies showing M1 activity do not employ electrophysiological monitoring to exclude muscle contractions during actual scanning.

In addition to the methodological differences, there has been some diversity among the behavioral tasks studied as motor imagery (Grezes and Decety 2001). Motor imagery is defined as the mental simulation of a motor act (Crammond 1997; Decety 1996; Jeannerod 1994). This definition can include various concepts such as preparation for movement, passive observations of action, and mental operations of sensorimotor representations, either implicitly or explicitly. Motor imagery as preparation for immediate movement likely involves the motor executive brain regions including M1, since M1 plays a significant role in sensory processing for the purpose of up-coming movement generation (Georgopoulos 2000). Implicit mental operations of sensorimotor representations, on the other hand, are considered to underlie cognitive functions such as mental rotation of body parts (Bonda et al. 1995; Parsons et al. 1995; Sekiyama et al. 2000) and mental calculations of abacus experts (Hanakawa et al. 1999). It is unclear whether a motor executive area such as M1 is active not only during motor preparation but also during mental operations of sensorimotor representations.

Another issue regarding neuroimaging studies on motor imagery is that the performance of imagination is notoriously difficult to control. To date, most studies have relied on subjective evaluation, rather than objective confirmation, of task performance. However, some neuroimaging studies on mental rotation or mental operations have successfully evaluated behavioral performance without involving any motor response during task periods (Hanakawa et al. 2002; Mellet et al. 1996; Richter et al. 1997). In these studies, subjects follow sensory

stimuli given serially to update mental representations during the task, and then report the final image at the end of the task. In the present study, application of this task design allowed us to explore, for the first time to our knowledge, brain activity during explicit mental operations of finger representations with objective confirmation of performance. Specifically, epochs for a motor imagery task were followed by a brief response period, during which subjects reported the final image of sensorimotor representation. This information was also used to explore brain areas associated with the task performance.

In the present study, fMRI was used to measure blood-oxygenation–level-dependent changes as an index of neural activity (Logothetis et al. 2001). Performance during motor imagery was objectively confirmed by comparing sensory-guided execution of sequential finger tapping with mental operations of equivalent sensorimotor representations. To exclude possible muscle contractions during motor imagery and to capture them during motor execution and responses, muscle activity was electronically monitored during actual MRI acquisition. Statistical parametric mapping revealed brain areas predominantly related to motor execution or motor imagery, and areas equally activated during both motor execution and imagery. By capitalizing on relatively fine temporal resolution, sustained activity during the motor execution and imagery task compared with transient activity related to the response movement was also analyzed (time-course analysis). The time-course analysis helped characterize the functional property of each set of areas from a different perspective, suggesting a functional gradation from more "executive" to more "imaginative" areas.

METHODS

Subjects

Ten healthy volunteers [mean age, 32 ± 11 (SD) years; males = 7, females = 3] participated in this study after giving informed consent approved by the institutional review board. All were right handed (laterality index = 0.7 ∼ 1.0) as assessed by Edinburgh Inventory (Oldfield 1971). None had a history of any neuropsychiatric disorders.

Behavioral tasks

NUMBER-GUIDED SEGMENTED SEQUENTIAL FINGER TAPPING TASK. Subjects performed a finger-tapping task with their right hand in either a movement or an imagery mode of performance. Visually presented number stimuli (number 1, 2, or 3) that specified a segment of a finger tapping sequence guided the task throughout. For the movement mode, subjects actually executed the tapping movement as briskly and distinctly as possible. For the imagery mode, subjects were asked to imagine the corresponding tapping movement being performed by them (first person perspective) as opposed to the movement being performed by someone else (Ruby and Decety 2001), without any accompanying overt movement.

Before the fMRI experiment, subjects completed a standardized training session (lasting approximately 1 h). First, subjects learned a simple sequential tapping movement (thumb-index-middle-ring-little-ring-middle-index. . .). Subjects thereafter practiced to start tapping from a finger specified by a cue stimulus and to proceed on the sequence according to a series of the number stimuli. All visual stimuli were presented visually on a computer monitor. The task began with the presentation of the cue stimulus for 2 s, which specified the first finger to start tapping (e.g., "MIDDLE" for middle finger). Subjects always started tapping from the radial side to
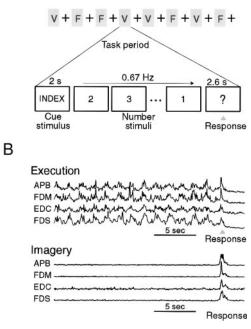

FIG. 1. *A*: experimental design for functional MRI (fMRI). Each fMRI run consisted of 8 task periods (dark gray, 31.2 s), alternated with 8 baseline periods (pale gray, 27.6 s) during which subjects fixated on a cross mark (+) flashing on and off at a rate of 0.67 Hz. The varied stimulus type (*V*) and the fixed stimulus type (*F*) were semi-randomly assigned to the task periods, while the movement mode and imagery mode were examined in the different runs (3 runs for each mode). During each task period, the cue stimulus (e.g., "INDEX" for the index finger) was presented for 2 s, which specified the first finger to start tapping from. A series of 17 number stimuli was then presented at a rate of 0.67 Hz and specified the segment of predetermined tapping sequence to be performed physically or mentally in response to each number stimulus. At the end of the task period for both modes, a question mark was presented for 2.6 s and prompted subjects to report the finger to be tapped next. *B*: electromyographic finding from a representative subject. Illustrated data were rectified and averaged over different blocks. Muscle activity was monitored from four muscles (abductor pollicis brevis, flexor digiti minimi, extensor digitorum communis, flexor digitorum superficialis).

the ulnar side, except when the little finger was specified by the cue stimulus. A series of 10 number stimuli, consisting of number 1, 2, or 3, were then presented one-by-one for 750 ms at a rate of 0.67 Hz (17 number stimuli were used for the fMRI experiment). Each number specified a segment of the finger tapping sequence, by instructing subjects to proceed on the tapping sequence by the amount of the presented number. Suppose that a cue stimulus was "INDEX", and number 2 and then 3 followed. When the cue stimulus was presented, subjects knew that they would start tapping from the index finger and waited for the first number stimulus in a ready state. As soon as the first number stimulus 2 was presented, subjects should tap the index and then middle finger, corresponding to the sequence segment of "index-middle." Following the number 3 presentation, therefore, subjects should tap the ring, little, and again ring fingers in this order. This process was repeated until the last number stimulus was presented. At the end, a question mark was presented, which prompted subjects to report the next finger they were ready to tap. In this task, as long as subjects have completely followed the instructions, they should be ready for a specific finger out of five fingers (probability of a correct response occurring by chance is 20%). Understanding of the operational principles was double-checked by visual inspection of movements during the task as well as the report of the "ready-to-tap" finger at the end.

After completing a set of training sessions in the movement mode, subjects were told that exactly the same principles were applicable to

the imagery mode. Subjects completed a set of the task in the imagery mode, in which many subjects tended to move their fingers at the beginning of training. However, all of them eventually succeeded in performing the task without visible finger movement. Objective assessment of the task performance in the imagery mode was made possible by the responses at the end of the task.

The primary interest of the present experiment was difference and similarity of brain activity between these two performance modes. The secondary interest of the present study was effects of two different types of the number stimuli (varied and fixed stimulus type) on brain activity. The number stimuli were randomly selected from the numbers 1 through 3 for the varied type and were always the number 2 for the fixed type. We assumed that the different stimulus types would introduce different levels of stimulus-dependency to the task, because subjects were able to perform the task with prediction for the fixed stimulus type after the training but they still had to rely on the number stimuli for the varied stimulus type. The number of tapping movement during a task period was on average balanced between the two stimulus types.

VISUAL FIXATION TASK. A visual fixation task was employed as a baseline condition for the fMRI experiment. Subjects were instructed to keep fixating on a cross that roughly matched the number stimuli in size and was presented for 750 ms at a rate of 0.67 Hz. During the visual fixation task, subjects were asked to clear their mind and withhold any movement except for physiological ones (i.e., natural blinking).

fMRI and electrophysiological monitoring

The fMRI experiment was conducted on a 1.5-T GE/SIGNA scanner with a standard quadrature head coil (GE Medical Systems, Milwaukee, WI). To reduce head motion during scanning, a bite bar made of a dental impression material was custom-made for each subject and fixed to a cradle of the head coil. Subjects lay supine on a scanner bed with a response device fixed to them at the wrist joint that had five buttons, one for each finger of the right hand. The subjects viewed visual stimuli back-projected onto a screen through a mirror built into the head coil, but were unable to see their hands during the fMRI experiment. The stimulus presentation was controlled by SuperLab (Cedrus, Phoenix, AZ) on a Power Macintosh computer (Apple Computer, Cupertino, CA). To avoid confusion, the execution and imagery modes of performance were investigated in different fMRI runs (3 runs for each mode, 6 runs in total). Each fMRI run, corresponding to single continuous acquisition of fMRI time series, lasted for 8 min and 30 s. The order for performance modes was pseudo-randomized across subjects. A single fMRI run started with a dummy run for 10.4 s, followed by a task period (31.2 s) alternated with a baseline period for the visual fixation task (28.6 s) eight times in blocks (i.e., 8 task periods per run; Fig. 1A). Each task period started with presentation of a cue stimulus (2 s), followed by 17 number stimuli presented at a rate of 0.67 Hz. The two stimulus types were semi-randomly assigned to the task periods (i.e., 4 task periods for each stimulus type) within a run. Therefore the whole fMRI session (48 task periods per subject in total) contained 12 task periods each for the varied stimulus-movement mode, fixed stimulus-movement mode, varied stimulus-imagery mode, and fixed stimulus-imagery mode. At the end of each task period, a question mark was presented visually for 2.6 s, during which subjects needed to press a button corresponding to the "ready-to-tap" finger for both performance modes. The responses from subjects were recorded through the response device. For the fMRI experiment, these responses were used to determine the accuracy of task performance for both of the movement and imagery modes.

T2* sensitive, three-dimensional functional images were acquired using principles of echo shifting with a train of observations sequence (PRESTO) (van Gelderen et al. 1995). Acquisition parameters were as follows: image acquisition = 2.6 s, data matrix = 64 × 51 × 32, voxel size = 3.75 mm^3 (see van Gelderen et al. 1995 for technical details of this scanning sequence). For a single fMRI run, 196 functional images were acquired. For the anatomical co-registration, we obtained high-resolution PRESTO images (data matrix = 192 × 153 × 96, voxel size = 1.25 mm^3) as well as T1-weighted, three-dimensional, fast spoiled gradient-recalled at steady-state images (data matrix = 256 × 256 × 124, voxel size = 0.94 × 0.94 × 1.5 mm).

Surface electromyograms (EMGs) were monitored from the right hand and forearm muscles using fMRI compatible equipment (Ives et al. 1993). Pairs of Grass gold electrodes were placed on the right abductor pollicis brevis, flexor digiti minimi, extensor digitorum communis, and flexor digitorum superficialis muscles. Interelectrode distance was approximately 3 cm. Surface EMGs were amplified, digitized (sampling rate, 250 Hz), and filtered with a band-pass of 30–70 Hz. EMGs were continuously monitored during fMRI acquisition by one of the authors (K.T. or M.A.D.) and stored on a hard drive for subsequent review.

Image analysis

Image analysis was performed using statistical parametric mapping (SPM99, http://www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (MathWorks, Natick, MA). The first four functional images (corresponding to the dummy run) were discarded to allow for T1 equilibrium effects; the remaining images were realigned to the first remaining image. All images were spatially transformed to fit to an in-house PRESTO template, which is compatible with the Montreal Neurological Institute (MNI) template (Evans et al. 1993), based on the stereotaxic coordinate system of Talairach and Tournoux (1988). To make the in-house template image, high-resolution PRESTO images were transformed to fit to the standard template provided by SPM99, averaged across 10 subjects, and smoothed with a Gaussian filter of 4-mm full-width at half-maximum (FWHM). During the spatial normalization process, functional images were resampled into voxels that were 2 × 2 × 2 mm in the x (right-left), y (rostral-caudal), and z (dorsal-ventral) directions. All functional images were then smoothed with a 7-mm^3 FWHM Gaussian kernel. Both individual and group analyses were performed by a multi-regression analysis (fixed effect model). Box-car functions representing the task epochs plus delta functions and their temporal derivatives modeling the response events, both convolved with the canonical hemodynamic response function, served as regressors of interests for a multiple regression analysis. A regressor representing the cue events was also included within the model. The time for the response events was calculated from the logged time for the button-press events during each response period. The mean difference between sessions was removed as a block effect, and the global difference between the scans was removed by scaling. Planned linear comparisons were performed to assess the main effect of performance modes (movement- or imagery-predominant activity), the main effect of stimulus types, and interaction terms, yielding statistical parametric maps of t-statistics. A conjunction analysis was employed to detect brain areas activated during the task equally for both performance modes (movement-and-imagery activity) (Price and Friston 1997). Significance level was set at a height threshold of $P < 0.05$ with correction for multiple comparisons. A more liberal threshold, $P < 0.001$ without correction, was used to pick up brain areas showing a nonnegligible trend toward activation. The estimated spatial resolution of the group analysis was 11.8 × 11.4 × 11.7 mm FWHM in the x, y, and z directions, respectively. To report activity, we converted the MNI coordinates into the Talairach coordinates using a linear transformation matrix and listed the Talairach coordinates. Activated areas were then localized as best as possible to the system of Brodmann (1909). We also listed the most likely functional area for each activity, if possible, as a reference for the nomenclature used for the time-course analysis.

TABLE 1. *Brain areas activated more during the movement tasks than the imagery tasks*

Cluster Size	Locations (Brodmann area), Functional Areas	x	y	z	Z-Value	P Corrected
1876	L precentral gyrus/knob (4), M1	−36	−23	49	Inf.	0.000
	L precentral gyrus (4/6), PMdc	−46	−15	52	Inf.	0.000
1881	R anterior cerebellum	20	−53	−19	Inf.	0.000
	Cerebellar vermis	4	−66	−7	Inf.	0.000
210	L parietal/temporal operculum (40/42), S2	−51	−26	14	Inf.	0.000
379	L anterior cerebellum	−28	−42	−25	7.79	0.000
265	Medial frontal gyrus (6), SMAc	−2	−4	46	6.82	0.000
15	L superior parietal lobule (5)	−24	−47	66	6.51	0.000
30	R posterior central gyrus (1, 2, 3)	53	−26	53	5.56	0.000

Cluster size = number of voxels; x, y, z = stereotaxic coordinates; P corrected = voxel level significance corrected for multiple comparisons; inf. = infinite.

Brain activity associated with task performance was explored in a separate hypothesis-driven analysis. Task blocks were divided into successful blocks and failed blocks. All of the image data were then reanalyzed using regressors representing these task blocks as well as the response events. A simple subtraction contrast was used to find brain areas showing more activity in the successful performance versus the failed performance within each domain of performance. Search volume was limited within the areas where either movement- or imagery-related activity was present (inclusive mask, threshold $P < 0.05$, uncorrected). Significance level was set at a height threshold of $P < 0.05$ with correction for multiple comparisons. A more liberal threshold, $P < 0.001$ without correction, was used to pick up brain areas showing a nonnegligible trend toward activation.

Finally, we carried out a time-course analysis on a subject-by-subject basis to investigate data from a different perspective, by examining a temporal profile of signal changes related to the tasks and response events. The time course analysis was performed by setting up a spherical volume of interest (VOI) with a 3-mm diam and the center at the local maximum activity based on a t-score. To define the local maximum activity in each individual, a contrast representing the effect of the execution task compared with the fixation task was used, except for the imagery-predominant areas where a contrast representing the effect of imagery task was used. The threshold was set at $P < 0.001$ without correction. Anatomical location of the activity peak was then determined by referencing the individual's PRESTO anatomical image. The location of the VOIs in three-dimensional sterotaxic space was estimated from the samples at 95% confidence level. We employed this approach (functionally determined regions of interest) because the conventional anatomically determined regions of interest that sometimes cover several gyri likely include several distinct functional areas. Note, however, that any sort of area-of-interest analysis, including the present one, depends on the knowledge of the functional neuroanatomy available at that time, and may be subject to future revision, especially in terms of anatomical nomenclature. We assigned

functional areas to each activity as best as possible, based on our current knowledge on the human functional neuroanatomy. For example, M1 was defined as activity close to or on the "knob"-like structure on the precentral gyrus in the central sulcus (Yousry et al. 1997). The caudal part of dorsal lateral premotor area (PMdc) was defined as activity on the precentral gyrus, which was lateral and rostral to the M1 activity and most frequently on its lateral convexity. Activity in the superior precentral sulcus at the level of the superior frontal sulcus or most caudal part of the superior frontal sulcus was designated as the rostral part of dorsal lateral premotor area (PMdr) (Hanakawa et al. 2002). Activity in the medial frontal cortex was classified into the rostral and caudal parts of supplementary motor areas (SMAr and SMAc, respectively), by whether it was anterior or posterior to the vertical anterior commissure line of the stereotexic coordinates (Deiber et al. 1991).

Signal changes were calculated from all suprathreshold voxels within each VOI, and were consolidated for each subject by averaging the signals across the repetitions of the tasks. Mean signal changes were then converted into percent signal changes by dividing the signal value of each scan by the averaged signal value from four scans (10.4 s) for the baseline before each task onset. To describe one type of activity in the time-course analysis, we will use the term "transient activity" to describe brief brain activity that can be modeled by the canonical hemodynamic response function. For the transient activity, therefore, we examined the time-course data, looked back to the multi-regression analysis that included two event-type regressors (for the cue stimulus presentation and response), and examined if the
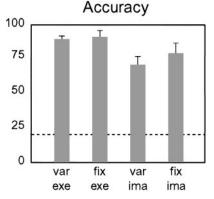

FIG. 2. Accuracy of task performance. In all conditions, accuracy was well beyond the chance level (dotted line). There was a significant main effect of the performance mode, which was execution or imagery.
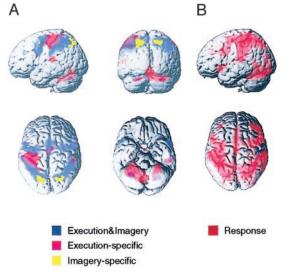

FIG. 3. Statistical parametric maps rendered over a standard anatomical brain. *A:* areas activated equally during the movement and imagery modes, areas predominantly activated during the movement mode, and areas predominantly activated during the imagery mode. *B:* areas showing activity significantly associated with response movements.

TABLE 2. *Brain areas activated equally during the movement and imagery tasks*

Cluster Size	Locations (Brodmann area), Functional Areas	x	y	z	Z-Value	P Corrected
3593	L intraparietal sulcus (40/7)	−44	−42	57	Inf.	0.000
	L supramarginal gyrus (40)	−38	−43	37	Inf.	0.000
1401	L superior precentral sulcus (6), PMdr	−38	−1	55	Inf.	0.000
	L inferior precentral sulcus (6/44), PMv	−56	3	29	Inf.	0.000
2445	R intraparietal sulcus (40/7)	48	−40	54	Inf.	0.000
1959	R superior precentral sulcus (6), PMdr	37	1	57	Inf.	0.000
	Medial frontal cortex (6), SMAr	−2	8	49	Inf.	0.000
75	R posterior cerebellum	30	−65	−22	Inf.	0.000
53	L posterior cerebellum	−32	−67	−24	Inf.	0.000
40	L middle frontal gyrus (9/46), DLPFC	−42	38	26	Inf.	0.000
32	L inferior frontal gyrus (47)	−51	−18	−4	Inf.	0.000
35	R inferior frontal gyrus (47)	51	17	−4	6.92	0.000
26	L fusiform gyrus (18), visual association area	−28	−90	−6	6.75	0.000
7	L putamen	−24	−4	2	5.03	0.001

Cluster size = number of voxels; x, y, z = stereotaxic coordinates; P corrected = voxel level significance corrected for multiple comparisons; inf. = infinite.

activity was correlated with the canonical hemodynamic response function.

RESULTS

Behavioral data

Task solutions reported by button press movements evaluated the accuracy of task performance. For the data from 10 subjects, repeated-measures ANOVA revealed a significant main effect of the performance mode [$F(1,9) = 6.85$, $P = 0.028$], indicating that task performance was less accurate in the imagery mode than the movement mode (Fig. 2). The effect of stimulus type was close to the significance level [$F(1,9) = 4.88$, $P = 0.054$]. There was no significant task mode-by-stimulus type interaction [$F(1,9) = 1.13$, $P = 0.32$]. Surface EMG monitoring clearly detected muscle activity during the movement mode, while it only detected muscle activity corresponding to the button press movements during the imagery mode (Fig. 1*B*).

Statistical parametric maps: effects of performance mode and stimulus type

A fixed-effect model group analysis revealed brain areas more involved either in the movement or imagery mode as well as those commonly involved in both modes. Brain areas activated more strongly during the movement mode than the imagery mode ($P < 0.05$ corrected) included the M1, PMdc, SMAc, parietotemporal operculum, anterior parietal cortex (area 5), and anteromedial part of the cerebellum (Table 1; Fig. 3*A*). The primary somatosensory cortex (S1) was very likely included in the cluster of activation in the left central area,

although S1 did not reveal its own peak activity in the group analysis. The temporoparietal operculum most likely corresponded to the second somatosensory cortex (S2). Among these movement-predominant brain areas, cerebral cortical structures exclusively involved the left hemisphere contralateral to the movement while cerebellar structures predominantly involved the right hemisphere.

The brain areas equally activated during the movement and imagery modes (movement-and-imagery areas by conjunction analysis, $P < 0.05$ corrected) was comprised of the dorsolateral prefrontal cortex, PMdr, SMAr, inferior precentral sulcus probably corresponding to the ventral lateral premotor area (PMv) or the posterior part of Broca's area, intraparietal sulcus (IPS) and supramarginal gyrus of the parietal cortex, basal ganglia, and posterolateral part of the cerebellum (Table 2; Fig. 3*A*). These structures were bilaterally symmetrical, but the activity was slightly lateralized to the left. Activity for the occipital visual areas was only slight, which suggested that activity associated with the low-level visual effects of the number stimuli was roughly controlled by the baseline visual fixation task.

Brain areas activated more during the imagery mode than the movement mode ($P < 0.05$ corrected) were localized to the bilateral posterior superior parietal cortex/precuneus and a small zone in the left precentral sulcus at the level of middle frontal gyrus (PcS/MFG) (Table 3; Fig. 3*A*). Areas rostral to the PMdr and SMAr tended to show higher activity during the imagery mode rather than the execution mode ($P < 0.001$, uncorrected).

Brain areas related to the button-press response movement ($P < 0.05$ corrected) consisted of widely distributed structures including the dorsolateral prefrontal cortex, PMv, PMdr/c,

TABLE 3. *Brain areas activated more during the imagery tasks than the movement tasks*

Cluster Size	Locations (Brodmann area), Functional Areas	x	y	z	Z-Value	P Corrected
150	L dorsal parietal cortex/precuneus (7)	−24	−69	53	6.21	0.000
94	R posterior superior parietal cortex/precuneus (7)	22	−69	53	6.04	0.000
6	L precentral sulcus/middle frontal gyrus (6)	−47	4	48	5.10	0.006

Cluster size = number of voxels; x, y, z = stereotaxic coordinates (Montreal Neurological Institute template); P corrected = voxel level significance corrected for multiple comparisons; inf. = infinite.

TABLE 4. *Brain areas activated in relation to response movement*

Cluster Size	Locations (Brodmann area), Functional Areas	x	y	z	Z-Value	P Corrected
11011	L inferior parietal lobule (40)	−44	−42	57	Inf.	0.000
	R inferior parietal lobule (40)	48	−42	56	Inf.	0.000
	R precuneus (7)	16	−71	51	Inf.	0.000
	L superior precentral sulcus (6), PMdr	−36	−1	57	Inf.	0.000
	L precentral sulcus/knob (4), M1	−38	−26	53	Inf.	0.000
	L inferior precentral sulcus (6), PMv	−53	3	29	Inf.	0.000
3085	R superior precentral sulcus (6), PMdr	34	1	57	Inf.	0.000
	Medial frontal gyrus (6), SMAc	0	−2	48	Inf.	0.000
	R middle frontal gyrus (9), DLPFC	36	44	29	Inf.	0.000
	Anterior cingulate cortex (24), CMAr	4	27	32	Inf.	0.000
	Medial frontal gyrus (6), SMAr	4	12	55	Inf.	0.000
6702	L posterior cerebellum	−20	−77	−18	Inf.	0.000
	R anterior cerebellum	32	−55	−20	Inf.	0.000
	R inferior occipital gyrus (18)	36	−87	3	Inf.	0.000
	L inferior occipital gyrus (18)	−28	−93	3	Inf.	0.000
	R cuneus (17)	12	−77	9	Inf.	0.000
	L cuneus (17)	−8	−83	8	6.38	0.000
89	L anterior cerebellum	−30	−67	−22	Inf.	0.000
96	R posterior cerebellum	32	−59	−24	Inf.	0.000
62	L middle temporal gyrus (21)	−51	−18	−4	Inf.	0.000
40	L supramarginal gyrus (40)	−40	−37	30	Inf.	0.000
51	R middle temporal gyrus (21)	51	−18	−2	7.38	0.000
34	R middle frontal gyrus (46), DLPFC	44	38	24	6.38	0.000
16	L putamen	−24	−5	2	5.58	0.001
12	L globus pallidus	−21	−13	−3	5.57	0.001

Cluster size = number of voxels; *x, y, z* = stereotaxic coordinates; *P* corrected = voxel level significance corrected for multiple comparisons; inf. = infinite.

SMAr/c, M1, S1, S2, IPS, precuneus, visual areas, and the cerebellar hemisphere (Table 4; Fig. 3*B*). These structures encompassed virtually all areas observed during the movement mode and/or imagery mode of the task. The response-related activity was bilaterally symmetrical but there was predominant activity on the left for PMdc, M1, S1, and S2, and on the right for the prefrontal cortex.

When activity during the varied stimulus presentation was compared with activity during the fixed stimulus presentation, only small zones in the inferior precentral sulcus ($x, y, z = −51, 9, 29$; area 6; Z-value = 4.87; 6 voxels) and the precuneus ($x, y, z = −22, −67, 51$; area 7; Z-value = 4.84; 9 voxels) showed significant stimulus-type effects. However, when the analysis was limited to the imagery mode, the zone in the inferior precentral sulcus, probably corresponding to PMv or the posterior part of Broca's area, showed a robust cluster with significant stimulus-type effects ($x, y, z = −55, 9, 29$; area 6; Z-value = 6.01; 54 voxels). No areas showed significant interaction between the performance modes and stimulus types.

Statistical parametric maps: activity associated with task performance

Activity associated with the accuracy of performance in the movement mode (successful vs. failed movement performance) was situated in the left area 5 and right anteromedial cerebellum where movement-predominant activity was found (Table 5; Fig. 4*A*). Activity associated with the imagery performance (successful vs. failed imagery performance) was located in the movement-and-imagery areas, extending into the imagery-predominant areas (Table 5; Fig. 4*B*). These areas included the bilateral superior precentral sulcus, including PMdr and PcS/MFG, as well as left IPS. SMAr and right IPS showed a trend toward difference in activity between the successful versus failed imagery performance ($P < 0.001$, uncorrected).

Time course analysis

The location of the VOIs is summarized in Table 6. In the frontal cortex, there appeared to be a transition from more

TABLE 5. *Activity associated with task performance*

Cluster Size	Locations (Brodmann area), Functional Areas	x	y	z	Z-Value	P Corrected
Movement mode						
733	L superior parietal lobule (5)	−38	−42	61	9.53	0.000
310	R anterior cerebellum	42	−59	−18	5.61	0.000
Imagery mode						
322	L precentral sulcus/middle frontal gyrus (6)	−40	−2	54	5.41	0.001
	L superior precentral sulcus (6), PMdr	−22	0	48	4.08	0.327
522	L intraparietal sulcus (40/7)	−44	−37	42	4.97	0.010
362	R precentral sulcus/middle frontal gyrus (6)	48	0	46	4.70	0.033

Cluster size = number of voxels; *x, y, z* = stereotaxic coordinates; *P* corrected = voxel level significance with correction for multiple comparisons.
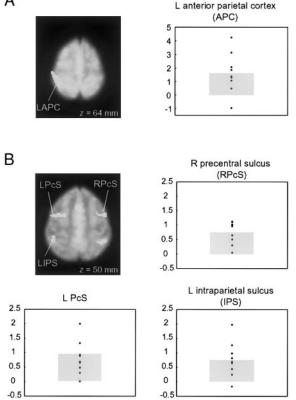
FIG. 4. Activity associated with accuracy of task performance. *A:* anterior parietal cortex (area 5) showed greater activity in the successful execution performance than in the failed one. Graph shows the size of effect (estimated difference in activity expressed in percentage) between the success and failure. Bar and dots represent mean and each individual's difference in activity, respectively. *B:* areas showing activity greater in the successful imagery performance compared with the failed imagery performance. Bilateral frontal zones were situated in the precentral sulcus and the left parietal zone was situated in the intraparietal sulcus (IPS). Areas without label (rostral part of supplementary motor area and right IPS) showed a trend but did not reach significance.

"executive" areas posteriorly to more "imaginative" areas anteriorly (Fig. 5). The posterior frontal parts, typically M1, showed marked activity during the movement mode but little activity during the imagery mode. When activity was carefully examined for each individual, only 1 of 10 subjects showed significant activity in M1 during the imagery mode of performance. The lack of significant activity in M1 at a group level during the imagery mode was further substantiated by the transient signal increase following the response movement present also for the imagery mode. This also suggested that the response-related activity might contribute to formation of the second peak in the temporal profile of M1 activity during the movement mode. Among the posterior frontal cortex, however, PMdc and SMAc exhibited mild yet clear sustained activity increase (approximately 0.2%) during the imagery mode. The rostral portions of the nonprimary motor areas, SMAr and bilateral PMdr, revealed more prominent imagery-related activity than did the caudal nonprimary motor areas, resulting in virtually the same temporal profile across the two modes. In PMdr, activity was more prominent in the left hemisphere compared with the right hemisphere. The dorsolateral prefrontal cortex and PcS/MFG also exhibited a temporal profile similar across the two performance modes; however, the im-

agery-related activity was exaggerated slightly in the dorsolateral prefrontal cortex and markedly in PcS/MFG as compared with the movement-related activity, representing the most imaginative area in the frontal cortex.

In the parietal cortex, conversely, there was a more of a transition from executive areas in the anterior part to imaginative areas in the posterior part (Fig. 6). S1 and S2, like M1, clearly showed sustained movement-related activity and transient response-related activity but no sustained imagery-related activity. Area 5, where the activity reflected the performance of the movement mode, showed marked movement- and response-related activity plus substantial imagery-related activity (approximately 0.7%). The middle portion of the parietal association cortex (IPS and supramarginal gyrus) exhibited similar activity across the two modes, predominantly in the left hemisphere, resembling the pattern observed in the rostral part of the nonprimary motor areas. The posterior superior parietal cortex/precuneus was characterized by bilaterally symmetric imagery-predominant activity. For the movement mode, on the other hand, activity in the posterior superior parietal cortex/ precuneus yielded a biphasic pattern of activity. This is because there was transient activity following the cue stimulus presentation or task initiation. This biphasic pattern of activity

TABLE 6. *Mean location of the areas of interest for time-course analysis*

Areas of Interest	Stereotaxic Coordinates (SD)			
	x	y	z	N
Frontal cortex				
L primary motor area (LM1)	−38 (4)	−26 (4)	53 (5)	10
L caudal dorsal premotor area (LPMdc)	−48 (9)	−15 (5)	50 (5)	10
Caudal supplementary motor area (SMAc)	−3 (6)	−6 (7)	54 (9)	10
L rostral dorsal premotor area (LPMdr)	−36 (7)	−1 (7)	58 (5)	10
R rostral dorsal premotor area (RPMdr)	36 (7)	0 (5)	58 (7)	10
Rostral supplementary motor area (SMAr)	−2 (4)	2 (8)	54 (8)	10
L dorsolateral prefrontal cortex (PFC)	−42 (6)	40 (3)	25 (9)	9
L precentral sulcus/middle frontal gyrus (LPcS/MFG)	−45 (10)	2 (7)	44 (6)	10
L inferior precentral sulcus (IPcS)	−50 (7)	2 (8)	30 (7)	9
Parietal cortex				
L primary somatosensory cortex (LS1)	−47 (6)	−28 (5)	52 (5)	9
L second somatosensory cortex (LS2)	−54 (7)	−27 (8)	16 (6)	9
L anterior parietal cortex (area 5)	−34 (7)	−41 (6)	64 (6)	10
L intraparietal sulcus (LIPS)	−42 (6)	−42 (6)	54 (8)	10
R intraparietal sulcus (RIPS)	44 (7)	−40 (9)	55 (9)	10
L supramarginal gyrus (LSMG)	−41 (6)	−42 (3)	34 (4)	8
L posterior superior parietal cortex/precuneus	−18 (8)	−53 (7)	54 (7)	10
R posterior superior parietal cortex/precuneus	−9 (5)	−63 (7)	58 (6)	10
Cerebellum				
R anterior cerebellum (RaCbll)	25 (6)	−50 (7)	−23 (5)	10
R posterior cerebellum (RpCbll)	31 (6.3)	−64 (6)	−22 (4)	9

N indicates the number of the subjects who exhibited supra-threshold voxels ($P < 0.001$, uncorrected) in each area.
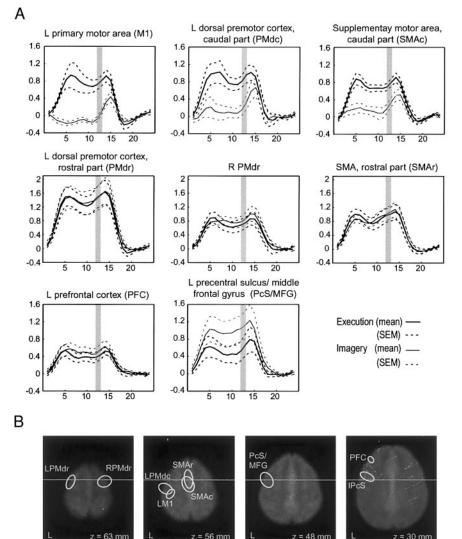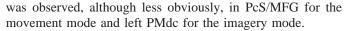
FIG. 5. *A*: time-series data from areas of interest in the frontal cortex. Figure shows the mean signal change across 10 subjects and SE. Time course data are aligned at the onset of task period (scan 1 of the abscissa). The abscissa indicates the number of scans (each scan lasted 2.6 s), and the ordinate indicates signal changes in percentage. Gray-shaded zone indicates the period of time allotted to the response for a behavioral report. *B:* areas served as volume of interest for the time course analysis in the frontal cortex, superimposed on an axial slice of the in-house PRESTO template image. Each oval represents a 95% confidence ellipse that summarized the location of peak activity from each individual. See also Table 5.

was observed, although less obviously, in PcS/MFG for the movement mode and left PMdc for the imagery mode.

In the right cerebellar hemisphere, there was sustained activity in the anteromedial part during the movement mode and only transient activity following the responses during the imagery mode, similar to the activity observed in M1 and S1. The posterolateral portion revealed almost equal activity for motor and imagery modes.

In the inferior precentral sulcus, activity revealed a similar time course between the movement and imagery modes (Fig. 8*A*). When the effect of stimulus type was examined, activity was greater for the varied stimulus type than for the fixed stimulus type, especially during the imagery mode (Fig. 8*B*). This activity showing stimulus-type effects typically occupied the inferior precentral sulcus, which possibly involved the caudal part of Broca's area. Moreover, this area corresponded to the area where the stimulus type effect was significant within the imagery mode of the performance as revealed by the statistical parametric mapping analysis (Fig. 8*C*).

To summarize these observations, a ratio reflecting relative weight on the imagery mode versus movement mode was calculated for each area from the mean activity averaged over the 5th through 10th scans (mean imagery/movement activity; Fig. 9).

DISCUSSION

Task design and behavioral performance

The movement and imagery tasks were based on the same operational rules and stimuli, and obviously shared many processes. These included visual information processing, conversion of the visual information to motor engrams according to arbitrary stimulus-response linkage, working memory, and monitoring instructed versus ongoing imagery/movement. Any mistake in these processes would result in failure to reach the correct answer for either task. The behavioral data, nevertheless, showed that the task performance was more accurate for the movement mode than for the imagery mode. This suggested that different more than common components of the two modes affected the task performance. For the movement mode, the performance would rely primarily on motor control based on the somatosensory feedback in reference to the instructed movement. For the imagery mode, on the other hand, the task
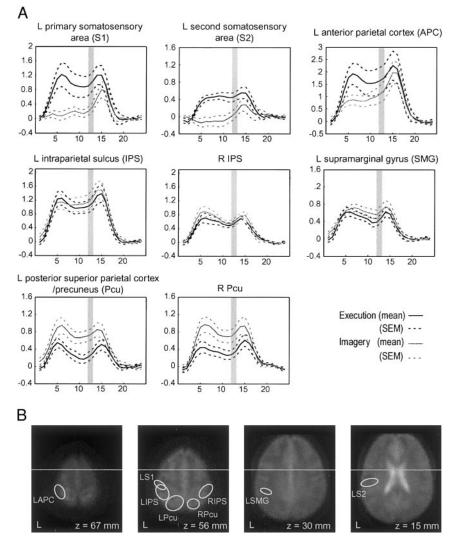
FIG. 6. *A:* time-series data from areas of interest in the parietal cortex. *B:* areas served as volume of interest for the time course analysis in the parietal cortex. See Fig. 5 for the display convention.

performance probably reflects success or failure in maintaining or upgrading mental finger representations in reference to the instructions.

For the difference in stimulus type, subjects tended to perform the tasks better for the fixed stimulus type than for the varied stimulus type that required higher stimulus dependency. This might be especially true in the imagery mode for which subjects probably need more mental resources than for the movement mode, although this idea was not completely supported by the behavioral data (i.e., mode-by-stimulus interaction was not significant).

The results showed widespread response-related activity, reflecting many cognitive-motor processes involved in the button-press responses. This observation raises a concern about the ubiquitous assumption in neuroimaging experiments. This assumption is that subtraction of activity during a control sensorimotor task from activity during a cognitive task plus responses would reflect activity due to the cognitive task. However, such a subtraction may lead to false activation that merely reflects a difference between the complicated responses and simple movements because the response-related activity was widely present in the "nonmotor" areas including the dorsolateral prefrontal cortex.

Functional neuroanatomy underlying motor execution and imagery

Statistical parametric mapping analysis showed the involvement of M1, PMdc, SMAc, area 5, parietotemporal operculum, anteromedial part of the cerebellar hemisphere, and cerebellar vermis more for movement than for motor imagery. Cerebral cortical activity was basically contralateral to the movement side, while the cerebellar activity was predominantly ipsilateral to it. This pattern is consistent with the previous neuroimaging observations that these structures primarily relate to movement execution (Deiber et al. 1998; Gerardin et al. 2000; Stephan et al. 1995). No previous study has thus far explicitly tested the conjoint effect of activity during movement and imagery tasks. The conjunction analysis revealed that both modes of the present task, movement and imagery, widely activated the frontoparieta areas and parts of cerebellum. This finding appears to agree with a notion that there is a substantial overlap between the motor simulation and execution in terms of underlying neural correlates. However, Gerardin et al. (2000), who employed relatively simple movement and imagery tasks, found imagery-predominant activity for many of the frontoparietal regions categorized into the execution-and-imagery areas in the present study. This discrepancy is probably because of
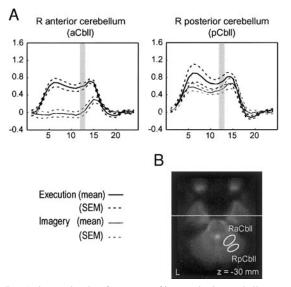
FIG. 7. *A*: time-series data from areas of interest in the cerebellum. *B:* areas served as volume of interest for the time course analysis in the cerebellum. See Fig. 5 for the display convention.

the difference in the task design between the two studies. In the present experiment, many sensory-cognitive components were required to monitor behavioral status with regard to the sensory instructions for both performance modes. Note, therefore, that the motor-and-imagery activity reflected not only the commonality between movement and motor imagery but also the sensory-cognitive components common to the two performance modes, which is an obvious limitation of the present study to explore the commonality between movement and imagery. Recently, to overcome this limitation, we examined brain activity during a task with an instructed delay between the number stimuli and motor execution/imagery, which has appeared in a preliminary form (Hanakawa et al. 2001) and will be discussed elsewhere.

Based on the behavioral evaluation, we explored brain areas associated with successful versus failed performance. The results revealed performance-related brain structures specific to each task mode. Area 5 shown for the movement mode is consistent with an idea that performance in this mode primarily reflects somatosensory-motor organization. The premotor-posterior parietal structures shown for the imagery mode suggest that these areas are important for operating mental finger representations according to external information.

Statistical parametric mapping is a very powerful tool in neuroimaging. This method does not necessarily require a specific hypothesis about regions but does require a hypothesis to design a general linear model analysis (i.e., a hypothesis about activity changes over time in fMRI time-series). The VOI-based time-course analysis complemented the statistical parametric mapping analysis and characterized well the slightly different behavior of the areas categorized into a single entity (i.e., movement-predominant areas) in the statistical parametric mapping analysis. The results further suggested a functional gradation, rather than the complete segregation, of the activity associated with movement and imagery (see Fig. 9). This evidence supports the idea proposed by Brooks (1986) that there is a transition from idea to action mediated by frontal-limbic circuits and

medial motor areas, occurring as a gradient. A result from a previous study already indicated a functional gradation from motor imagery to action in the medial frontal motor areas (i.e., SMAr and SMAc) (Tyszka et al. 1994), although the functional gradation concept has not been as much discussed compared with the concept parceling functional areas. The present work has provided evidence to support the functional gradation concept for wider brain areas related to movement and motor imagery.
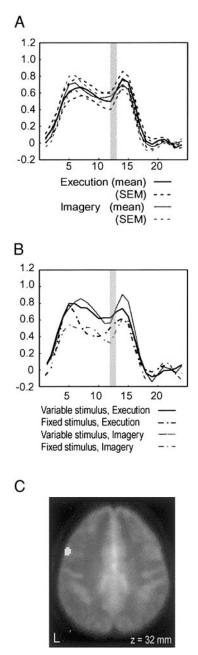

FIG. 8. *A*: time-series data from part of the inferior precentral sulcus, consistent with Broca's area. See Fig. 5 for the display convention. *B*: time-series data averaged for the motor execution task and imagery task, taking into account the difference in the stimulus type. *C*: activity in the inferior precentral sulcus showing a significant stimulus-type effect for the motor imagery task, superimposed on an axial slice of the PRESTO template image, as revealed by statistical parametric mapping analysis.
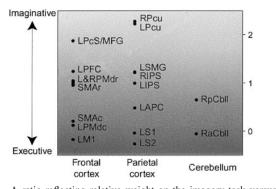
FIG. 9. A ratio reflecting relative weight on the imagery task versus execution task calculated from the mean activity averaged over the 5th through 10th scans (mean imagery activity/mean execution activity). The greater the ratio is, the greater the imagery-related activity is (i.e., more "imaginative") in reference to the execution-related activity.

Frontal cortex

In the time-course analysis, the VOI only covering activity on the hand "knob" structure in the precentral gyrus was defined as M1. M1 showed sustained activity during the movement mode but not during the imagery mode, and revealed transient activity corresponding to the button-press responses for both performance modes. The dissociation between the imagery-related activity and response-related activity, best characterized in the time-course analysis, primarily indicated that M1 activity was exclusively related to immediate movement. Although there is evidence that M1 computes sensory information (Georgopoulos 2000), this computation is most likely to prepare for upcoming movements. Some fMRI studies have detected a mild increase in activity in the posterior part of the precentral gyrus during motor imagery (Lotze et al. 1999; Porro et al. 1996; Roth et al. 1996). Because these studies lack EMG monitoring during actual MR scanning, the effect of mild muscle contractions cannot be entirely excluded. Alternatively, the discrepancy may be due to the difference in the experiment design; for example, a control task such as visual imagery possibly induces a slight deactivation in the task-irrelevant brain areas. More importantly in our opinion, when a region of interest encompasses the convexity part of the precentral gyrus, it likely reflects activity of parts of Brodmann area 6 in addition to that of M1 (Preuss et al. 1996; Rizzolatti et al. 1998). Actually, PMdc defined here as the convexity part of the precentral gyrus revealed a sustained increase in activity during motor imagery. In any event, a human lesion study suggests that M1 does not play a fundamental role in motor imagery (Sirigu et al. 1995), although individual subjects may show M1 activity during motor imagery depending on their strategy.

SMAc exhibited activity similar to that of PMdc: mild activity during motor imagery and much greater activity during movement, both followed by transient activity for the response events. PMdc and SMAc are both considered the caudal parts of the "nonprimary motor" or "premotor" areas (Geyer et al. 2000; Picard and Strick 2001; Preuss et al. 1996; Rizzolatti and Luppino 2001; Rizzolatti et al. 1998). Anatomical studies in nonhuman primates have shown that the PMdc, SMAc, and parts of the anterior cingulate cortex directly project to M1 and the spinal cord, and it is thus likely that these caudal premotor areas directly relate to the generation of overt movement (He et al. 1993, 1995). The mild activity increase in PMdc and SMAc

during the imagery mode suggests a role of these areas in motor imagery as well, and further implies a functional difference among the areas categorized into a single entity as the movement-predominant areas.

In contrast to the caudal parts, the rostral parts of the nonprimary motor areas were similarly active in both performance modes. The increased activity of SMAr has been reported for motor imagery tasks (Deiber et al. 1998; Gerardin et al. 2000; Ruby and Decety 2001; Tyszka et al. 1994) as well as higher-level motor control (Deiber et al. 1991; Picard and Strick 1996). PMdr shown in the present study corresponds to the area that is particularly active for movement requiring spatially complex structure (Catalan et al. 1998; Hanakawa et al. 2002; Sadato et al. 1996) and for movement requiring more complex stimulus-response linkage (Grafton et al. 1998). PMdr, as defined in the present study, is probably consistent with the "prePMd" recently proposed by Picard and Strick (2001). PMdr and SMAr do not directly project either to M1 or the spinal cord; instead, they are closely connected to the prefrontal cortex (He et al. 1993, 1995; Luppino et al. 1993). The prefrontal cortex, SMAr, and PMdr actually revealed very similar temporal profiles in activity changes for both modes, suggesting the similar functional role of the rostral premotor parts with the prefrontal cortex rather than the motor executive, caudal premotor areas and M1. Activity of SMAr and PMdr during cognitive tasks supports this idea (Fiez et al. 1996; Hanakawa et al. 2002). It is likely that the prefrontal cortex plays a role in holding sensory information on-line so that the ongoing behavior is consistent over time (Fuster 2001).

A part of the inferior precentral sulcus, probably corresponding to PMv, also showed similar activity across both performance modes. This zone may correspond to the rostral part of the PMv, or area F5 in nonhuman primates, which has a motor representation of the hand (Rizzolatti et al. 1998). In the present experiment, this activity extended rostrally into Broca's area pars opercularis (area 44), the possible homologue of a subdivision of area F5 (Rizzolatti and Arbib 1998). This particular subdivision of F5 contains the so-called "mirror" neurons that discharge when monkeys perform an action and also when they observe another individual making the same action (di Pellegrino et al. 1992). The property of these neurons is suggested as a basis of the matching system between observations and actions, which probably plays a role in the present tasks that require constant monitoring of instructed versus ongoing imagery/movement. Note that the effect of stimulus variability on motor imagery, which had not been explored previously, was only reflected in this area. Our hypothesis was that the varied stimulus type would demand more sensory dependent-type of motor imagery than the fixed stimulus type, which would in turn impose higher demands on the matching system between the instructed versus ongoing imagery. An alternative explanation is that the varied stimuli require more subvocalization of the number stimulus.

Activity associated with the task performance for the imagery mode was localized in the precentral sulcus in the frontal cortex, indicating the significance of this region in motor imagery. There are several possible interpretations for imagery-predominant activity. The PcS/MFG zone that also showed imagery-predominant activity may correspond to one of the "negative motor areas" where electrical stimulation causes cessation of movement (Luders et al. 1995) because activity for

inhibiting movement would be needed during motor imagery. However, the negative motor area in the lateral frontal area is situated in the inferior frontal gyrus, which is ventral to the PcS/MFG zone. Alternatively, the PcS/MFG activity may correspond to the frontal eye fields (Desmurget et al. 2000), located probably ventrolateral to PMdr in the precentral sulcus at the middle frontal gyrus level in humans (Hanakawa et al. 2002). It is less likely, however, that this activity is due to actual eye movement because subjects needed to keep fixating on the center of view. This region is often activated during tasks involving spatial attention but not necessarily involving eye movements (Corbetta 1998; Hanakawa et al. 2002; Hopfinger et al. 2000; Mellet et al. 1996). Removal of this area induces reluctance to use the contralateral hand and hemi-inattention (Rizzolatti et al. 1983). Together, the PcS/MFG activity may relate to attention to the contralateral hand possibly represented in the self-centered or hand-centered coordinate system.

Parietal cortex

Activity in the anterior parts of the parietal cortex, such as S1 and area 5, most likely reflects somatosensory-motor association and sensory feedback from muscles and joints inherent to overt movement (Mima et al. 1999), both of which are components of the movement mode, but obviously not of the imagery mode. Among these parietal movement-predominant areas, however, only area 5 showed moderate imagery-related activity. Moreover, activity of the area 5 was significantly associated with the task performance of the movement mode, supporting the important role of somatosensory-motor integration in the movement mode of the task. The area 5 likely corresponds to the parietal area PE, which is regarded as a higher-order somatosensory area mostly devoted to analyzing proprioceptive information. Area PE primarily connects with M1 and provides information about location of body parts necessary for movement control (Rizzolatti et al. 1998).

The middle part of the parietal cortex, the supramarginal gyrus and IPS, showed sustained activity during both modes. The part of ventral premotor area F5 where "mirror" neurons exist constitutes a circuit with the parietal area PF (Rizzolatti et al. 1998), and PF is thought to correspond to the supramarginal gyrus in humans (Grezes and Decety 2001). IPS is composed of multiple subdivisions in nonhuman primates, and each subdivision constitutes a circuit with the subdivisions of the frontal premotor areas (Rizzolatti and Luppino 2001; Rizzolatti et al. 1998). The movement-and-imagery activity in the middle portion of the parietal cortex was considerably lateralized to the left hemisphere. This activity, together with the activity in the precentral sulcus, was significantly correlated with the task performance. Left parietal lesions involving the supramarginal and angular gyri relates to the development of impaired motor attention (Rushworth et al. 1997) and Gerstmann's syndrome, characterized by acalculia, agraphia, finger agnosia, and right-left disorientation (Benton 1992). Moreover, detailed neuro-psychological examination supports the role of the parietal cortex in generating mental movement representations (Sirigu et al. 1996).

The posterior part of the parietal cortex, including the precuneus, has been reported to be active during tasks involving motor imagery, implicitly (Bonda et al. 1995; Hanakawa et al. 1999; Parsons et al. 1995) or explicitly (Ruby and Decety 2001). The imagery-predominant activity agreed with a recent study showing the overactivity of the posterior parietal cortex during motor imagery of finger movement than during execution (Gerardin et al. 2000). It is reported that the precuneus, together with the frontal precentral sulcus zone, subserves spatial information processing and attention (Corbetta 1998; Hopfinger et al. 2000; Mellet et al. 1996). This parietal subdivision might correspond to the parietal area V6a in nonhuman primates (Rosa and Tweedale 2001). As opposed to object-motion detected by area V5, area V6a may function to detect self-motion. Area V6a also has a putative role in directing skeletomotor activity to extrapersonal space.

Subcortical areas

The sensory information processing for feedback motor control partly explains movement-predominant activity in the anteromedial cerebellar hemisphere and vermis (Gao et al. 1996). However, part of this activity probably reflects a feedforward-type of motor control or internal models of the motor apparatus (Kawato and Gomi 1992), because movement-related cerebellar activity can be observed in patients with severe sensory impairment (Weeks et al. 1999). These cerebellar "motor" regions receive inputs from spinocerebellar pathways, and from M1 and S1 via the pons, and then project back to M1. The cerebellar movement-and-imagery activity was located posterolaterally to the movement-predominant cerebellar activity. This dissociation of the motor-related and "nonmotor"-related cerebellar activity is consistent with a previous neuroimaging observation (Allen et al. 1997). There is supportive anatomical evidence from nonhuman primates that different parts of the cerebellum form multiple closed-loop circuits with distinct areas of the cerebral cortex (Middleton and Strick 2000). The basal ganglia contralateral to the performance side were also detected as movement-and-imagery activity.

In conclusion, the results from this study have provided evidence to support the concept of functional gradation from more imaginative properties to more motor executive properties in many cortical and subcortical areas. The most executive areas coincided with the motor areas that directly send output to M1 or the spinal cord or the areas associated with sensory feedback processing and somatosensorimotor association. However, some of the movement-predominant areas also showed imagery-related activity, supporting a functional gradation from imagery to movement. Many areas in the frontoparietal cortex and posterolateral cerebellum showed similar activity between the movement and imagery modes that share multiple components of the tasks. The areas most active with imagery (PcS/MFG, precuneus) may reflect a requirement of motor inhibition or attention to hand-centered space. The left frontoparietal areas correlated with the imagery task performance can be considered the primary basis of sensory-guided motor imagery studied in the present study. Finally, the effect of stimulus variability on motor imagery was observed in the inferior precentral sulcus, suggesting importance of the matching system between the ongoing and the instructed behavior.

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