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Imagery of Voluntary Movement of Fingers, Toes, and Tongue Activates Corresponding Body-Part–Specific Motor Representations

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Ehrsson, H. Henrik, Stefan Geyer, and Eiichi Naito. Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part–specific motor representations. *J Neurophysiol* 90: 3304–3316, 2003; 10.1152/jn.01113.2002. We investigate whether imagery of voluntary movements of different body parts activates somatotopical sections of the human motor cortices. We used functional magnetic resonance imaging to detect the cortical activity when 7 healthy subjects imagine performing repetitive (0.5-Hz) flexion/extension movements of the right fingers or right toes, or horizontal movements of the tongue. We also collected functional images when the subjects actually executed these movements and used these data to define somatotopical representations in the motor areas. In this study, we relate the functional activation maps to cytoarchitectural population maps of areas 4a, 4p, and 6 in the same standard anatomical space. The important novel findings are *1*) that imagery of hand movements specifically activates the hand sections of the contralateral primary motor cortex (area 4a) and the contralateral dorsal premotor cortex (area 6) and a hand representation located in the caudal cingulate motor area and the most ventral part of the supplementary motor area; *2*) that when imagining making foot movements, the foot zones of the posterior part of the contralateral supplementary motor area (area 6) and the contralateral primary motor cortex (area 4a) are active; and *3*) that imagery of tongue movements activates the tongue region of the primary motor cortex and the premotor cortex bilaterally (areas 4a, 4p, and 6). These results demonstrate that imagery of action engages the somatotopically organized sections of the primary motor cortex in a systematic manner as well as activating some body-part–specific representations in the nonprimary motor areas. Thus the *content* of the mental motor image, in this case the body part, is reflected in the pattern of motor cortical activation.

INTRODUCTION

Humans can imagine that they are performing a movement without actually executing it. This cognitive state is called *motor imagery* and can be experienced by most people (Annett 1995; Crammond 1997; Jeannerod 1994). The essential component of motor imagery is that the subject imagines himself or herself to be executing the action from the first-person perspective. Examples of motor imagery are the imagined movement of isolated limbs, the imagined movement of the whole body, imagined manipulation and interaction with objects in one's environment, and mental rehearsals of the kind used by sportsmen and musicians (Annett 1995; Feltz and Landers 1983; Jeannerod 1997).

During motor imagery, memory information related to previous enactments is retrieved (Annett 1996). It has been suggested that these "motor memories" are stored in the motor system (Naito et al. 2002a; Nyberg et al. 2001; Rijntjes et al. 1999; Roland et al. 1993a). Similarly, in the last two decades it has been a common view that motor imagery corresponds to a type of motor preparation process where motor programs are recruited to simulate motor performances without executing the movements (e.g., Jeannerod 1994, 1995; Roland et al. 1980). The "simulation hypothesis" of motor imagery, which has been established by psychophysical and neuroimaging evidence in human subjects (see following text), states that motor imagery of an action involves the recruitment of the same neural networks in the motor system that are engaged when the movement is actually being executed (Decety 1996; Jeannerod 1994, 1995). Psychophysical experiments have shown that imagined movements seem to obey the same "motor rules" (e.g., speed-accuracy trade-off) and biomechanical constraints as real movements (Danckert et al. 2002; Decety and Jeannerod 1996; Decety and Michel 1989; Decety et al. 1989; Frak et al. 2001; Jeannerod 1994; Johnson 2000a,b; Papaxanthis et al. 2002; Parsons 1987, 1994; Parsons and Fox 1998; Sirigu et al. 1996).

Likewise, functional imaging studies have shown that motor imagery of various types of hand actions rather consistently activates most areas associated with sensorimotor control: typically activation is reported in the supplementary motor area (SMA), the cingulate motor areas (CMAs), the premotor cortex, Broca's area and its right homolog (areas 44 and 45), and the posterior parietal cortex (Binkofski et al. 2000; Decety et al. 1994; Deiber et al. 1998; Gerardin et al. 2000; Hanakawa et al. 2003; Ingvar and Philipson 1977; Lotze et al. 1999; Naito et al. 2002a; Rao et al. 1993; Roland et al. 1977, 1980; Ruby and Decety 2001; Stephan et al. 1995; Thobois et al. 2000). The involvement of the tentative hand section of the primary motor cortex (M1) is less consistent across studies: some investigators report increases in activity in the precentral gyrus and central sulcus (tentative M1) during motor imagery (Leonardo et al. 1995; Lotze et al. 1999; Porro et al. 1996; Roth et al.

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1996; Sabbah et al. 1995), whereas others, often using positron emission tomography (PET), fail to detect any significant effect (Binkofski et al. 2000; Decety et al. 1994; Deiber et al. 1998; Gerardin et al. 2000; Naito et al. 2002; Ruby and Decety 2001; Stephan et al. 1995).

An important prediction of the simulation hypothesis is that imagery of *different* types of movement should engage the different corresponding motor representations. Here we test this prediction by asking subjects to imagine that they are making movements of different body parts. The rationale for manipulating the body part in the motor image is that the cortical representation of different body parts can be anatomically distinguished with functional imaging techniques (e.g., Ehrsson et al. 2000; Grafton et al. 1991; Rijntjes et al. 1999). We reasoned that if imagery of a particular movement engages the neural populations that control overt movements, one would expect that motor imagery of voluntary movements of different body parts would engage different somatotopical parts of the M1 and the nonprimary motor areas in a manner similar to that of movement execution.

We used functional magnetic resonance imaging (fMRI) to register regional increases in synaptic activity in the brain (Logothetis et al. 2001) and asked a single group of subjects to imagine that they were performing simple repetitive movements of their fingers, toes, and tongue, and to execute these actions as separate tasks. By contrasting these conditions directly, we could test whether motor imagery activates somatotopical motor representations. To localize synaptic activity in the M1 (which include areas 4a and 4p), the premotor cortex, and the SMA, we related the fMRI activations to cytoarchitectonically defined population maps of areas 4a, 4p, and 6 obtained from 10 postmortem human brains (Geyer et al. 1996, 2002). Preliminary results from this study were previously reported (Ehrsson et al. 1999, 2001a).

METHODS

Subjects

Six right-handed healthy males and one female (aged from 21 to 33 yr; with a mean age of 25) with no history of neurological disease participated in the study. The 7 subjects had given their written consent and the Ethical Committee of the Karolinska Hospital had approved the study, which was performed in accordance with the guidelines of the Declaration of Helsinki (1975). The subjects were also tested on a motor imagery test and they were all rated as having an average or good motor imagery ability (Naito 1994; Naito et al. 2002a; Nishida et al. 1986).

Conditions

There were 3 motor imagery conditions, 3 conditions where the subjects executed the movements, and 6 identical rest conditions (one rest condition being assigned to each imagery or execution condition). Before the brain scanning started, the subjects trained to perform all conditions (for 10 min in all) during which time we also recorded electromyograms (EMGs; see following text for details) and electrooculograms (EOGs).

For the movement execution conditions, for which the terminology MOVE FINGERS, MOVE TOES, and MOVE TONGUE is adopted, the subjects made repetitive brisk flexion/extension movements of their fingers and toes, or horizontal movements of their tongue. During the finger movement condition (MOVE FINGERS) the subjects repeatedly fully extended (digits II– V) and flexed their fingers through about 90° at the metacarpophalangeal joint. To make the toe movements (MOVE TOES), the subjects repeatedly flexed and extended their toes through their whole range of movement. Finally, during the tongue movements (MOVE TONGUE), the subjects made horizontal movements of the tongue from side to side within the mouth (with an estimated angle of about 30° to the right and 30° to the left). All movements were paced by an auditory metronome that generated a sound at 1-s intervals (1 Hz). At each sound, the fingers/toes were either maximally extended as instructed or maximally flexed as instructed. Likewise, at each metronome sound the tongue was either moved to the right or to the left as described above. In other words, each full cycle of flexion/extension or right/left tongue movement took 2 s. In all movement execution conditions the subjects were asked to relax completely and to make no movements other than those they were instructed to make.

For the 3 motor imagery conditions (designated IMAGINE FINGERS, IMAGINE TOES, and IMAGINE TONGUE), the subjects were instructed to imagine that they executed brisk alternating flexion/extension movements of the fingers and toes, or horizontal movements of the tongue. They were told to imagine generating the movements exactly as they had executed these in the overt movement conditions. The metronome paced the subjects, who were instructed to imagine that they were making the movements in time with the sound (at a frequency of 1 Hz), as in the execution conditions.

Finally, in the rest (REST) conditions, the subjects were instructed to relax completely, make no movements, and not to think about anything in particular while listening to the metronome (1 Hz). There were 6 identical rest conditions ($REST_1$, $REST_2$, $REST_3$, $REST_4$, $REST_5$, $REST_6$), each serving as an independent baseline for one of the movement/imagery conditions (as required in the "conjunction analyses"; see following text).

Training session and behavioral recordings during fMRI scanning

As mentioned in the text above, the subjects performed the motor imagery conditions in test sessions outside the magnetic resonance imaging (MRI) scanner, whereas EMGs were recorded from the flexor and extensor muscles of the right fingers (*m. flexor digitorum superficialis* and *m. extensor digitorum*) and right toes (*m. extensor digitorum brevis, m. flexor digitorum brevis*) (Myo115-electrodes; Liberty Technology, Hopkinton, MA). The EMG signals were stored and displayed on-line. We also recorded the eye movements using EOGs (Neuroline neurology electrodes, type 700 01-A 12; Ölstykke; gain: 2000; high-pass filter: 20 kHz).

During the brain scan the performance of the subjects was monitored on-line and recorded with a digital videocamera (Sony, digital videocamera recorder, DCR-TRV8E). After each run we asked the subjects to give a verbal description of how they had experienced the imagery and real movement conditions. In these reports, all subjects stated that they had generated vivid motor imagery for most of the time during all imagery conditions in all runs.

Brain scanning

While the brain scans were being performed, the subjects rested comfortably in a supine position on the bed in the MRI scanner. The extended arms and legs were oriented parallel to the trunk. The right arm was fully extended and the right leg was slightly flexed. Both the arm and leg were supported. The subjects did not wear socks or shoes on their right foot. A plastic bite bar, which had been fitted to each subject's teeth before scanning started, restricted head movements (the bite bar did not interfere with the tongue movements). They were instructed to have their tongue in a relaxed comfortable position inside their closed mouth. The room was dark and the subjects were blindfolded. All subjects wore headphones to reduce noise and to receive auditory cues.

Functional MRI was conducted on a 1.5-T scanner (Signa Horizon

Echospeed, General Electric Medical Systems, Milwaukee, WI) equipped with a head coil. We collected gradient-echo, echo-planar (EPI) T2*-weighted image volumes with blood oxygenation level–dependent (BOLD) contrast. The imaging parameters were: echo time (TE) = 60 ms; field of view (FOV) = 22 cm; matrix size = 64 × 64; pixel size = 3.4 × 3.4 mm; and flip angle = 90°. Twenty-one contiguous axial slices of 5 mm thickness were collected in each volume. These volumes covered the whole of the frontal and parietal lobes in all subjects. The cerebellum was outside the scanner's FOV, so we do not report on the eventual activity from this structure. A whole brain high-resolution T1-weighted anatomical MRI was also obtained for each subject (3D-SPGR).

Functional-image volumes were collected in 8 separate runs. In each run a total of 150 functional-image volumes was acquired continuously, with one volume being collected every 5,000 ms (TR = 5 s). The subjects performed the different tasks (and the rest condition) for periods of 30 s (6 fMRI volumes being collected in this time). The periods of the imagery and movement conditions were alternated with rest conditions to minimize possible fatigue-related effects (i.e., each imagery/execution condition was preceded and followed by rest conditions). Across runs, we alternated the order of the imagery and real movement conditions to reduce time effects. To allow for T1 equilibration effects, we started each experiment by recording 4 "dummy" volumes that were not stored. In total, 1,200 volumes were collected for each participant, with the same number of volumes being collected for each subject and condition.

Data analysis and image processing

SPM99 was used to preprocess and analyze the functional images (http//:www.fil.ion.ucl.ac.uk/spm). The functional images were realigned to correct for head movements (Ashburner and Friston 1997), whereupon they were coregistered with each subject's anatomical T1 MRI and subsequently normalized (linear and nonlinear transformations) into the reference system of Talaraich and Tournoux (Ashburner and Friston 1997; Talaraich and Tournoux 1988), using the Montreal Neurological Institute's (MNI) reference brain. The voxels were reformatted to obtain isometric voxels, spatially smoothed with an isotropic Gaussian filter of 9 mm full width at half-maximum (FWHM), and temporally smoothed with a Gaussian kernel of 5-s width, to conform to the Gaussian assumptions of SPM99 and to improve the signal-to-noise ratio. The images were scaled to 100 to eliminate the effects of global changes in the signal. A linear regression model [general linear model (GLM)] was fitted to the fMRI data from all subjects (Friston et al. 1995a,b; Holmes et al. 1997).

Because we had 7 subjects, we performed a fixed effect analysis and pooled the data across subjects to increase the sensitivity of the analysis. The validity of this approach in terms of the consistency of the effects across all the subjects in the group was confirmed by examining the activation patterns of individual subjects (see following text). Each task was modeled with a boxcar function that had been filtered with the standard SPM99 synthetic hemodynamic response function. The linear contrasts of the parameter estimates generated statistical parametric maps (SPM) of *t*-statistics (SPM *t*). To test for common activation across contrasts (conjunction analysis), the SPM *t* was combined from independent contrasts (and the SPM99 orthogonalization procedure was used) to generate a new SPM $t_{\min}$ that described the minimum *t*-value detected in the contrasts at each voxel (Worsley and Friston 2000). We reported only activations that, after a correction for the number of multiple comparisons in the whole brain space, corresponded to a $P < 0.05$ using a combined test for peak height (Friston et al. 1995b), or $P < 0.001$ using a test based on the minimum *t*-values observed in conjunction analyses (Worsley and Friston 2000).

We defined linear contrasts in the GLM to test our hypotheses. We first contrasted the imagery conditions with the rest conditions to reveal the general pattern of activity in the motor areas during imagery of movements of different body parts (see Fig. 1).

We then tested our main hypothesis that motor imagery of the movement of different body parts would engage different somatotopical zones of the motor areas. This was done in 3 steps. First, to directly test for body-part–specific activation during imagery we compared imagined movements of one body part with the imagined movements of the other 2 body parts [e.g., (IMAGINE FINGERS–IMAGINE TOES) and (IMAGINE FINGERS–IMAGINE TONGUE), respectively (see Fig. 2)]. Brain activity robustly associated with imagining the movement of a particular body part should be revealed in both these comparisons (we report only activations that fulfill this criterion). Second, by contrasting the movement execution conditions, we could define somatotopical sections of the motor cortices (Fig. 2) [e.g., the finger zones were

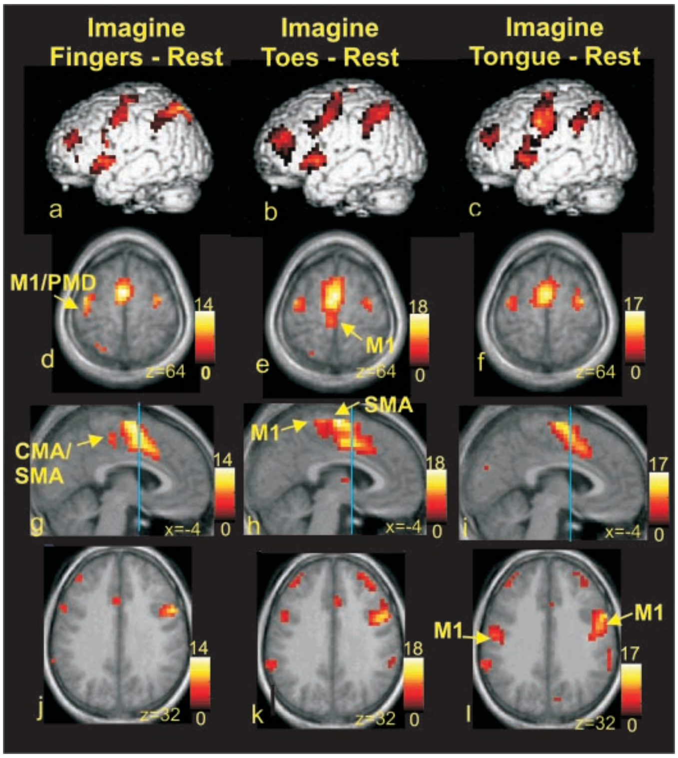

FIG. 1. Brain activation observed while subjects imagined they were making movements with their fingers (*left column*; *a, d, g, j*), toes (*middle column*; *b, e, h, k*), and tongue (*right column*; *c, f, i, l*) compared with resting baseline condition. General activation pattern was similar for 3 conditions with recruitment of a set of prefrontal, posterior parietal, and sensorimotor-related areas (*a–c*). However, differences in spatial distribution of activity in motor areas were observed (*d–l*). Imagery of finger movements activated a section of central sulcus (*d*) that was not active in other conditions (*e, f*). Likewise, paracentral lobule (foot M1) was active only when subjects imagined they were making toe movements (compare *h* with *g* and *i*) and central sulcus at level of tongue representation was active only in the IMAGINE TONGUE condition (compare *l* with *j* and *k*). In addition, a section of border zone between areas CMAc and SMA was activated only when subjects imagined they were moving their fingers (compare *g* with *h* and *i*) and a posterior section of SMA was active only during condition where only toes were imagined to be moved (compare *e* with *d* and *f*). For a demonstration of statistically significant differences in activation between different imagery conditions see Figs. 2 and 3. Activations, obtained in group analysis, are displayed on axial (*d–f, j–k*) or sagittal (*g–i*) slices of a mean image generated from anatomical T1-weighted MRIs from all subjects or a 3D-rendered image of standard brain (*a–c*). Coordinates (x, y, z) refer to standard space [Montreal Neurological Institute (MNI)]. We used threshold of $t = 3.09$ for statistical images; only activations that correspond to $P < 0.05$ after correction for number of multiple comparisons based on peak height are shown. (Results were also masked with corresponding imagery condition contrasted with rest condition at a voxelwise $t = 3.09$.)

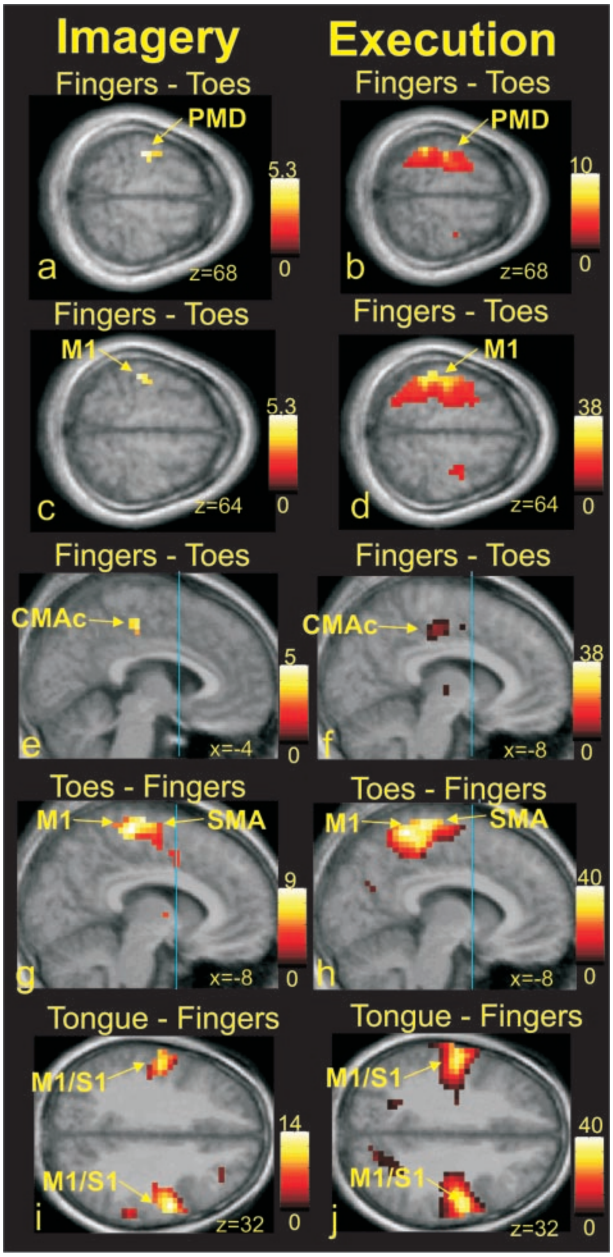

FIG. 2. Somatotopy of motor imagery. *Left column*: activation of different somatotopical sections of frontal motor areas when subjects were imagining they were performing voluntary movements of different body parts. *Right column*: finger, toe, and tongue regions defined by contrasting movement execution conditions. Arrows point to relevant imagery-related activations: imagery of finger movements activated left dorsal premotor cortex (PMD) (*a*, *b*), left primary motor cortex (M1) (*c*, *d*), and caudate cingulated motor area/supplementary motor area (CMAc/SMA) region (*e*, *f*); imagery of toe movements activated toe section of left M1 and left posterior part of SMA (corresponding to foot zone) (*g*, *h*); and imagery of tongue movements was associated with increases in activity in bilateral M1 and premotor cortex corresponding to tongue representation (*i*, *j*). Note especially good correspondence between somatotopic maps obtained by analyzing motor imagery conditions (*left column*) and movement execution conditions (*right column*). Activation maps obtained by other relevant contrasts (e.g., IMAGINE FINGERS–IMAGINE TONGUE) were virtually identical to those shown here (also see Table 1). Activations, obtained in group analysis, are displayed on axial (*a*–*d*, *i*, *j*) or sagittal (*e*–*h*) slices of a mean image generated from anatomical T1-weighted MRIs from all subjects. Coordinates (x, y, z) refer to standard space (MNI). We used threshold of $t = 3.09$ for statistical images; only activations that correspond to $P < 0.05$ after a correction for number of multiple comparisons based on peak height are shown. (Results were also masked with corresponding imagery condition contrasted with rest condition at a voxelwise $t = 3.09$.)

detected with the contrast (MOVE FINGERS–MOVE TOES)]. Third, we investigated whether these somatotopically organized areas corresponded exactly to those regions that were being activated in a body-part–specific manner during imagery. For this, we used a conjunction analysis (as described above) to test whether a voxel that showed body-part–specific activity during motor imagery also showed activity specific to the same body part during movement execution (these results are presented in Table 1). For example, to examine the specific involvement of the finger zones when the subjects were imagining that they moved their fingers, the conjunction analysis was used to test for voxels active in common in the 2 contrasts (IMAGINE FINGERS–IMAGINE TOES) and (MOVE FINGERS–MOVE TOES). We write these conjunction analyses as IMAGINE FINGERS–IMAGINE TOES $\cap$ MOVE FINGERS–MOVE TOES.

In the comparisons of the different movement execution and imagery conditions (i.e., all the contrasts defined in the text above), we restricted the results to voxels that were active in comparison with the rest condition (at $t > 3.09$ at each voxel using an inclusive masking procedure). [For example, for the contrast (IMAGINE FINGERS–IMAGINE TOES) we use an inclusive mask (IMAGINE FINGERS–REST).] With this masking procedure, we focused on sensorimotor-related brain areas that showed stronger activity during imagery of movement than when the subject was resting, and excluded the possibility that differences between the imagery conditions merely reflected different degrees of deactivation.

Activations in individual subjects

The statistical analysis was based on the functional data pooled across subjects; that is, the results of the group analysis were the statistically significant activations ($P < 0.05$ corrected). To display the activity at these sites we also show activations obtained by analyzing the data from individual subjects. There were 2 reasons for this: *1*) we wanted to make sure that the results obtained in the group analysis were representative for all 7 subjects; and *2*) we wanted to refine the way in which we anatomically localized the activations by making a direct comparison between the activation peaks in individual subjects with the corresponding high-resolution anatomical (T1-weighted) MRI. We display only the individual subject data from the most relevant contrasts—that is, those testing for differences in brain activity in the conditions where the subjects imagined that they were making movements of their fingers, toes, and tongue. In this purely descriptive analysis all image-processing steps were identical to those used in the group analysis, with the exception that we used a smaller spatial Gaussian filter (5-mm FWHM). The same GLM as in the group analysis was used, with the only difference that we considered the functional data from each subject separately. We report BOLD signals only from the regions that were found to be significantly active in the group analysis (as shown in Table 1). We probed for increases in the BOLD signal ($P < 0.05$ uncorrected) in a volume of radius 12 mm around the voxels, which corresponded to the peaks detected in the group analysis (with the radius of the volume being determined on the basis of the estimated smoothness of statistical images; Ehrsson et al. 2002; Naito et al. 2002b). We report the number of subjects showing a BOLD signal increase. To describe the variability of the location of the activations in the standard anatomical space and the variability of the observed *t*-values we report *1*) the mean *t*-value (±SD) of the local peaks of activity, *2*) mean coordinates in the standard anatomical space (x, y, z) of the local peaks, and *3*) the mean distance between the location of the activation peaks in the individual subjects and the location of the peak of activity in the group analysis (see Table 2).

Anatomical localizations and cytoarchitectural population maps

The fMRI activations were related to cytoarchitonically defined motor areas (Geyer et al. 1996; Schleicher et al. 1999). Primary

TABLE 1*a*. *Finger-specific activation during imagery*

	I.fin.–I.toe				I.fin–I.ton.				I.fin.–I.toe M.fin.–M.toe*				I.fin.–I.ton.∩ M.fin–M.ton.*			
Anatomical Region	x	y	z	t	x	y	z	t	x	y	z	$t_{\min}$	x	y	z	$t_{\min}$
Left superior frontal gyrus (SMA/CMAc)	0	−24	48	5.22	−4	−24	52	8.89	−4	−24	48	4.52	−4	−24	52	8.89
Left precentral gyrus (PMD, area 6)	−32	−24	68	4.89	−32	−24	68	3.33#	−32	−24	68	4.49	−32	−12	68	3.91
Left precentral gyrus (M1, area 4a)	−40	−28	64	4.51	−40	−28	64	3.38#	−40	−28	64	4.51	−40	−28	64	3.54

TABLE 1*b*. *Toe-specific activation during imagery*

	I.toe–I.fin				I.toe–I.ton.				I.toe–I.fin.∩ M.toe–M.fin*				I.toe–I.ton.∩ M.toe–M.ton.*			
Anatomical Region	x	y	z	t	x	y	z	t	x	y	z	$t_{\min}$	x	y	z	$t_{\min}$
Left paracentral lobule (M1, area 4a)	−8	−28	64	8.83	−8	−24	72	9.58	−8	−28	64	8.63	−8	−24	72	9.58
Left superior frontal gyrus (SMA, area 6)	−8	−20	72	8.00	−8	−20	72	9.32	−8	−20	72	8.00	−8	−20	72	8.00
Left putamen	−20	16	4	5.45	−28	12	−8	5.77	−28	12	−8	5.77	−28	12	8	5.77
Right putamen	28	8	4	5.19					32	8	4	3.92				
Right inferior frontal gyrus, pars opercul.	56	4	8	5.84	52	16	−8	6.09	56	8	4	4.91	56	8	0	3.95

TABLE 1*c*. *Tongue specific activation during imagery*

	I.ton.–I.fin.				I.ton.–I.toe				I.ton.–I.fin.∩ M.ton.–M.fin*				I.ton.–I.toe∩ M.ton.–M.toe*			
Anatomical Region	x	y	z	t	x	y	z	t	x	y	z	$t_{\min}$	x	y	z	$t_{\min}$
Left central sulcus (M1, border areas 4a and 4p)	−56	−12	32	14.13	−56	−12	32	15.15	−56	−12	32	14.13	−56	−12	32	15.15
Left central gyrus (M1/PM, border areas 6 and 4a)	−64	0	24	10.23	−68	−4	24	8.88	−64	0	24	10.23	−64	−4	24	8.88
Right central sulcus (M1, border area 4a and 4p)	56	−4	32	17.77	56	−4	28	17.91	56	−4	32	17.77	56	−4	28	17.91
Right precentral gyrus (PMD, area 6)	48	−12	56	8.99	52	−12	52	8.31	48	−12	56	8.99	52	−12	52	8.31
Right precentral gyrus (PMD)	32	−4	64	4.54	32	−8	64	5.70	24	−20	72	4.90	32	−8	64	5.70
Right putamen	28	0	−8	8.87	28	0	−8	6.76	28	4	−4	8.87	28	−4	−4	6.20

Significant local maxima of activation specifically associated motor imagery of finger movements (IMAGINE FINGERS–IMAGINE TOES), (IMAGINE FINGERS–TONGUE) ($P < 0.05$ corrected for multiple comparisons at the cluster level and at the voxel level). All regions were also active ($t = 3.09$ at each voxel) when the imagery condition was compared with the baseline condition (by a masking procedure). Only somatotopical zones of the motor regions that were consistently activated in association with imagination of one body part in comparison to both the other 2 effectors are shown. Anatomical locations were related to the mean standardized antomical MRI. I.fin., IMAGINE FINGERS; I.toe, IMAGINE TOES; I.ton., IMAGINE TONGUE; M.fin., MOVE FINGERS; M.toe, MOVE TOES; M.ton., MOVE TONGUE. Anatomical abbreviations: supplementary motor area (SMA), caudal part of the cingulate area (CMAc), dorsal premotor area (PMD), primary motor cortrex (M1), primary somatosensory cortex (S1), and premotor cortex (PM); * conjunction analysis in SPM99; # activation corresponding to $z > 3.09$ ($P < 0.001$ uncorrected). The activation did not reach the statistical criterion of $P = 0.05$ corrected.

motor areas 4a and 4p and the premotor area 6 (Geyer et al. 2002) were delineated in 10 postmortem brains. The borders between different cytoarchitectonic areas were determined subjectively and on the basis of statistically significant differences in the neuronal cell bodies (Schleicher et al. 1999). The brains were corrected for deformations arising from the histological processing and warped to the same reference brain of the computerized atlas as the fMRI images (Roland et al. 2001) using the full-multigrid (FMG) method (Schormann and Zilles 1998). A population map was generated for each area (Roland and Zilles 1998; Fig. 3). The population maps describe, for each voxel, how many brains have a representation of one particular cytoarchitectonic area. The individual variation in the location and extent of each cytoarchitectural area led to voxels representing more than one area. In these cases, the voxel was allocated to the cytoarchitectural area to which most of the brains represented in the voxel belonged (typically, voxels belonging to an area had a representation of that area in ≥30–40% of the brains). The result was a population map (Roland et al. 2001) of the cytoarchitectural areas (see Fig. 3). To define the borders between the population maps and the cortex for which we have no microstructural data (e.g., the rostral border of area 6) we adopted the criterion that a voxel had to be located in the microstructurally

TABLE 2. *Activation in individual subjects*

	Group-Analysis Peak			Subjects With Activation	Nearest Peak Activation ($P < 0.05$ Uncorrected)		
Motor Area	x	y	z	Number of Subjects	Mean *t*-Value (±SD)	Mean Location (x, y, z)	Mean Distance* (mm ± SD)
IMAGINE FINGERS–(IMAGINE TOES + IMAGINE TONGUE)							
Left superior frontal gyrus (SMA/CMAc)	0	−24	48	7/7	5.47 (2.2)	−2, −22, 50	6.1 (3.1)
Left precentral gyrus (PMD)	−32	−24	68	7/7	4.68 (2.49)	−32, −26, 66	6.8 (5.4)
Left precentral gyrus (M1)	−40	−28	64	7/7	5.21 (2.4)	−41, −28, 65	6.8 (3.1)
IMAGINE TOES–(IMAGINE FINGERS + IMAGINE TONGUE)							
Left paracentral lobule (M1)	−8	−28	64	7/7	6.36 (3.7)	−9, −34, 68	7.8 (4.0)
Left superior frontal gyrus (SMA)	−8	−20	72	7/7	5.81 (3.7)	−9, −19, 71	7.9 (4.0)
IMAGINE TONGUE–(IMAGINE FINGERS + IMAGINE TOES)							
Left central sulcus (M1)	−56	−12	32	7/7	7.19 (3.0)	−54, −11, 34	6.9 (2.3)
Left central gyrus (M1/PM)	−64	0	24	7/7	7.45 (2.4)	−60, −4, 25	9.9 (2.5)
Right central sulcus (M1/PM)	56	−4	32	7/7	7.69 (3.8)	57, −2, 29	5.3 (3.5)

Number of subjects showing activation ($P < 0.05$ uncorrected) in a region of interest (ROI$^{\#}$; a sphere of radius 12 mm) around the peak voxels detected in the motor cortices during the group analysis. The mean *t*-value, mean Talaraich coordinate, and the mean distance of the activation peaks from the group peak are reported. *t*-value = 1.65 ($P = 0.05$ uncorrected), 3.09 ($P = 0.001$ uncorrected), 4.59 ($P = 0.05$ corrected). For abbreviations see Table 1.

defined brain area in at least 3 of the 10 postmortem brains (Naito et al. 2002b). In cases when a voxel was allocated with the same likelihood to 2 areas (e.g., 30% of all brains had area 4a represented in this voxel and 30% had area 4p represented in the same voxel), we refer to this voxel as being located in the "border zone" between the 2 areas. The thresholds we adopted to generate the population maps (i.e., about 30–40% overlap) were used before and can be motivated on empirical grounds (e.g., Bodegard et al. 2001; Ehrsson et al. 2001b; Naito et al. 2001, 2002b). There is a high degree of intersubject variability in the location of the cytoarchitectural areas even after spatial normalization (Roland et al. 1997, 1998; Geyer et al. 2000). This means that if one uses high thresholds (e.g., 60–80% overlap), one ends up with gaps between the areas and this is anatomically meaningless because there is no "no-man's-land" in the brain. In contrast, thresholds of 30–40% give areas with reasonable volume without gaps between them.

Finally, we relate the locations of the local peaks of the activations to the cytoarchitectural population maps. We also describe the overlap between the activated clusters and the population maps (using Boolean intersection). (For further discussion of the technique of combining functional imaging and cytoarchitectural mapping, see Bodegard et al. 2001; Geyer et al. 2000; Naito and Ehrsson 2001; Naito et al. 2002b; Roland and Zilles 1998; and Roland et al. 2001).

The anatomical localization of the activations was also related to the major sulci and gyri distinguishable on a mean MRI generated from the standardized anatomical MRIs from the 7 subjects (Duvernoy 2000).

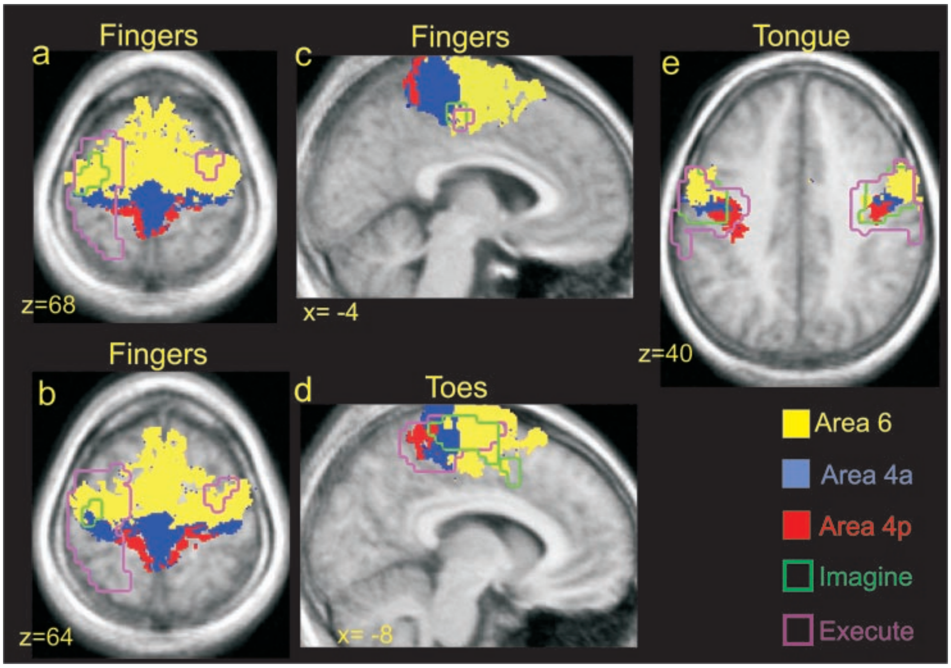

FIG. 3. Somatotopically organized areas activated during imagery superimposed on cytoarchitectonic population maps (Roland et al. 2001; see METHODS). Blue areas represent cytoarchitectonic area 4a; red areas, 4p; and yellow areas, 6. Green contour shows clusters of active voxels associated with imagery of finger movement (IMAGINE FINGERS–IMAGINE TOES; *a–c*), toe movements (IMAGINE TOES–IMAGINE FINGERS; *d*), and movements of tongue (IMAGINE TONGUE–IMAGINE FINGERS; *e*). Note that these clusters of active voxels are identical to those presented in Fig. 2 and for details about thresholds used see Fig. 2 legend. Purple contour corresponds to somatotopical sections of sensorimotor areas as defined by contrasting overt movement conditions (in *a–c*: MOVE FINGERS–MOVE TOES; in *d*: MOVE TOES–MOVE FINGERS; in *e*: MOVE TONGUE–MOVE FINGERS; $P < 0.05$ corrected). All clusters and cytoarchitectonic maps are displayed on a mean image generated from anatomical T1-weighted MRIs for all subjects.

RESULTS

Behavioral recordings

One concern in all studies of motor imagery is that the subjects might make small movements or weak muscular contractions during the imagery conditions. We are of the opinion that it should be possible to dismiss this concern because, in the training sessions conducted immediately before the brain scan, no muscular activity could be measured in the relevant muscles with the EMGs in any of the subjects when they imagined making the flexion/extension movements of their fingers and toes. Likewise, there were no significant differences in the number of eye movements between the imagery conditions, the movement execution conditions, and the rest periods, as determined by the EOGs (paired t-test $P > 0.05$). Furthermore, video recordings from the fMRI scanning sessions showed that the subjects never moved their limbs during the imagery conditions.

Motor imagery and motor execution compared with rest

Before examining the contrasts that directly test for a somatotopical activation pattern (described in the next paragraphs) we wanted to make sure that our results were consistent with the results of earlier functional imaging studies. For this purpose, we contrasted the finger motor imagery condition with the resting baseline condition to depict the general pattern of activity (Fig. 1).

When the subjects imagined that they were moving their fingers (IMAGINE FINGERS–REST), toes (IMAGINE TOES–REST), and tongue (IMAGINE TONGUE–REST) a bilateral set of frontoparietal areas was active: the precentral gyrus (mainly area 4a), sections of the bilateral SMA, the dorsal premotor cortex (PMD, area 6), the ventral premotor cortex (PMV, area 6), putamen, thalamus, dorsolateral prefrontal cortex, inferior frontal gyrus (pars opercularis and triangularis), intraparietal cortex, supramarginal cortex, and cuneus ($P < 0.05$ corrected; note not all areas and subcortical structures are displayed). This activation pattern is generally consistent with the results presented in earlier functional imaging studies (see the INTRODUCTION and Gerardin et al. 2000). As seen in Fig. 1, several of these areas were active in common when the subjects imagined movement of the 3 body parts. Importantly, however, the spatial distribution of activity in the motor areas was different in the 3 imagery conditions. As evident from Fig. 1, *d–l*, imagery of finger, toe, and tongue movement activated different sections of the M1. In the nonprimary motor areas, imagery of finger movement activated the caudal cingulate motor area (CMAc; Roland and Zilles 1996), the ventral part of the SMA (Fig. 1*g*), and a part of the PMD (not shown in Fig. 1). These sections were not active when subjects imagined toe or tongue movements. Likewise, imagery of toe movements activated toe-MI and a posterior part of the SMA that was not active when the subjects imagined that they were moving the other body parts (Fig. 1, *g–i*) and the tongue section of M1 was activated only when the subjects imagined the tongue movements (Fig. 1, *j–l*). In a paragraph below we present the results from the contrasts that directly test whether there are any statistically significant differences in the activation maps between the imagery conditions.

Movement execution and somatotopic mapping of the motor areas

We used the data from the conditions where the subjects actually executed the movements to define body-part–specific regions and somatotopic maps in the motor areas. This was done by contrasting the movement execution conditions (we used the contrasts MOVE FINGERS–MOVE TOES, MOVE TOES–MOVE FINGERS, and MOVE TONGUE–MOVE FINGERS). As seen in Fig. 2 (*right column*), we found a clear somatotopical organization in M1 where movement of fingers, toes, and tongue was associated with distinct clusters of active voxels (engaging both areas 4a and 4p). Likewise, in area 6, different representations for fingers, toes, and tongue were detected. These representations were located just rostral to the corresponding M1 representations. Thus a finger section of the lateral premotor cortex was observed rostral to the M1 finger zone, a tongue section of the premotor cortex located rostral to the tongue M1, and a toe representation of the supplementary motor area was detected rostral to the toe section of M1. We also observed somatotopic representations in the primary somatosensory cortex (S1) for all 3 body parts and a region specific to finger movement in the CMAc.

It can also be mentioned that we inspected the results obtained by contrasting the movement execution conditions and the rest condition (not shown). In these contrasts, the expected set of motor, somatosensory, and posterior parietal areas was activated (e.g., see Ehrsson 2002): the left M1, left S1, SMA, CMA, parietal operculum, anterior part of the intraparietal cortex and cortex of the postcentral sulcus, and the bilateral PMD, PMV, putamen, and thalamus (not shown). Parenthetically, it can also be noted that several areas showed activation both when subjects imagined the action and when they executed the same action: the left M1 (area 4a), bilateral SMA (area 6), CMA, PMD (area 6), PMV (area 6), intraparietal cortex, supramarginal cortex, putamen, thalamus, the right area 44, and the right insula ($P < 0.05$ using the SPM99 conjunction analysis; results not shown). This extensive overlap of areas active during movement execution and imagination is generally consistent with earlier fMRI studies (Gerardin et al. 2000; Hanakawa et al. 2003) and are not be discussed further in this communication (these authors did not find M1 activation).

Body-part–specific activations during imagery

To test the hypothesis that motor imagery of the movement of fingers, toes, and the tongue would be associated with different characteristic activation patterns in somatotopically organized motor areas, we defined contrasts where we directly compared the motor imagery conditions (e.g., IMAGINE FINGERS–IMAGINE TOES). We then tested whether the body-part–specific activations observed during the imagery conditions were located in the correct somatotopically organized sections of the motor cortex. This was done by directly relating the body-part–specific activations observed during imagery to the body-part–specific activations detected during the execution conditions by using a conjunction analysis (see METHODS and the text below for details).

Fingers

ACTIVATIONS SPECIFIC TO THE IMAGERY OF FINGER MOVEMENT (IMAGINE FINGERS–IMAGINE TOES), (IMAGINE FINGERS–IMAGINE TONGUE). Comparing the functional images for the imagination of finger movements with those for the imagination of either toe and tongue movements revealed 2 particularly important clusters of active voxels ($P < 0.05$ corrected). The 1st cluster was observed in the left precentral gyrus when the imagery finger movements were compared with imagery movements of the toes (IMAGINE FINGERS–IMAGINE TOES) (Table 1*a*; Fig. 2, *a* and *c*). Two significant local maxima of activity (peaks) could be distinguished. One peak of the activation was located on the crown of the left precentral gyrus ($x = -32$, $y = -24$, $z = 68$; see Fig. 2*a*). This peak corresponds to area 6 according to the cytoarchitectural population maps (30% of the brains had their area 6 represented at this site; see Fig. 3*a*). A 2nd peak was located in the upper part of the anterior bank of the left central sulcus ($x = -40$, $y = -28$, $z = 64$; Fig. 2*c*). This site corresponded to area 4a (Fig. 3*b*; 40% of the postmortem brains). We found BOLD signal increase at the area 6 and area 4a when the imagery of finger movement was contrasted with the imagery of tongue movements (IMAGINE FINGERS–IMAGINE TONGUE), but the increase did not reach the significance criterion after the correction for multiple comparisons ($P > 0.05$ corrected; $P < 0.001$ uncorrected; see Table 1*a*). In Fig. 4, where we plot the amplitude of the BOLD signals in area 4a, it can be seen that the M1 activation was weaker when subjects imagined finger movements compared to when they executed these movements and that there were virtually no activations in the other conditions (see Fig. 4).

The 2nd cluster was centered over the cingulate sulcus with the peak being located on the most ventral part of the mesial superior frontal gyrus (IMAGINE FINGERS–IMAGINE TOES, IMAGINE FINGERS–IMAGINE TONGUE; $x = 0$, $y = -24$, $z = 48$; see Fig. 2*e* and Table 1*a*). This peak was significantly active in the 2 contrasts (IMAGINE FINGERS–IMAGINE TOES) and (IMAGINE FINGERS–IMAGINE TONGUE). The location of this peak corresponds to the border between the most ventral part of medial area 6 (SMA) and the CMAc, which lies in the cingulate sulcus (see Fig. 3*c*).

SOMATOTOPIC FINGER ZONES SPECIFICALLY ACTIVE DURING THE IMAGERY AND EXECUTION OF FINGER MOVEMENT: (IMAGINE FINGERS–IMAGINE TOES∩MOVE FINGERS–MOVE TOES), (IMAGINE FINGERS–IMAGINE TONGUE∩MOVE FINGERS–MOVE TONGUE). To directly test whether a voxel that showed finger-specific activity during motor imagery also showed activity specific to the execution of finger movement, a conjunction analysis was used (see METHODS). This analysis revealed that the left M1 (area 4a), the left PMD (area 6), and the CMAc/SMA region were active in common during both the imagery and execution of finger movements in comparison to the imagery and execution of the other body parts (IMAGINE FINGERS–IMAGINE TOES∩MOVE FINGERS–MOVE TOES); (IMAGINE FINGERS–IMAGINE TONGUE∩MOVE FINGERS–MOVE TONGUE) ($P < 0.05$ corrected; see Table 1*a*).

Toes

ACTIVATIONS SPECIFIC TO THE IMAGERY OF TOE MOVEMENT (IMAGINE TOES–IMAGINE FINGERS), (IMAGINE TOES–IMAGINE TONGUE). The most conspicuous activation observed specifically during the imagery of toe movements was located in the left paracentral lobule (foot M1; $x = -8$, $y = -28$, $z = 64$; ≥40% of the postmortem brains had their area 4a located at this site), in the posterior part of the SMA (area 6; $x = -8$, $y = -20$, $z = 72$; ≥40% of the brains had area 6 represented here), the right inferior frontal gyrus (pars opercularis and pars triangularis), and in the bilateral putamen (see Fig. 2, *g* and *h*, Fig. 3*d*, and Table 1*b*). These regions were consistently active in the contrasts (IMAGINE TOES–IMAGINE FINGERS) and (IMAGINE TOES–IMAGINE TONGUE). As evident from Fig. 4, where we display the amplitude of the BOLD signals, the strongest signal increase was observed in the conditions where the subjects imagined or executed toe movements.

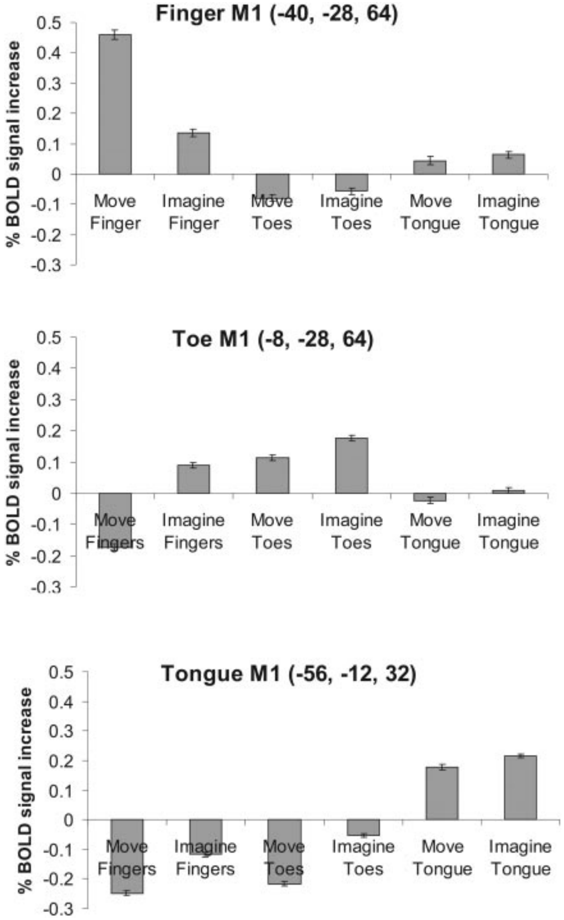

FIG. 4. Amplitude of blood oxygenation level–dependent (BOLD) signal increase in left M1 during imagery and execution of movements of fingers, toes, and tongue. Values correspond to adjusted BOLD signal (% increase) subtracted from rest condition. Data were pooled across 7 subjects. Error bars correspond to SE. Note somatotopic pattern of signal increases (significant at $P < 0.05$ corrected in statistical parametric map (SPM) analysis; see Fig. 2 and Table 1).

SOMATOTOPIC TOE ZONES SPECIFICALLY ACTIVE DURING THE IMAGERY AND EXECUTION OF TOE MOVEMENT (IMAGINE TOES–IMAGINE FINGERS∩MOVE TOES–MOVE FINGERS), (IMAGINE TOES–IMAGINE TONGUE∩MOVE TOES–MOVE TONGUE). The conjunction analysis showed that the sections of the left SMA, M1 putamen, and the right inferior frontal gyrus that were specifically active when subjects imagined making the toe movements were also active specifically during execution of toe movements (IMAGINE TOES–IMAGINE FINGERS∩MOVE TOES–MOVE FINGERS), (IMAGINE TOES–IMAGINE TONGUE∩MOVE TOES–MOVE TONGUE).

Tongue

ACTIVATIONS SPECIFIC TO THE IMAGERY OF TONGUE MOVEMENT (IMAGINE TONGUE–IMAGINE FINGERS), (IMAGINE TONGUE–IMAGINE TOES). When subjects imagined that they were moving their tongue, we observed stronger activity in the bilateral premotor cortex (area 6 in ≥30% of the postmortem brains), the bilateral cortex lining the central sulcus (the border between areas 4a and 4p; x = −56, y = −12, z = 32; x = 56, y = −4, z = 32), and the right putamen than when they imagined that they were performing movements with their fingers and toes (Table 1*c*, Fig. 2, *i* and *j*, and Fig. 3*e*) [areas consistently active in the 2 contrasts (IMAGINE TONGUE–IMAGINE FINGERS), (IMAGINE TONGUE–IMAGINE TOES)]. As seen in Fig. 4, it was only when the subjects imagined or executed the tongue movements that the bilateral M1 was active.

SOMATOTOPIC TONGUE ZONES SPECIFICALLY ACTIVE DURING THE IMAGERY AND EXECUTION OF TONGUE MOVEMENT (IMAGINE TONGUE–IMAGINE FINGERS∩MOVE TONGUE–MOVE FINGERS), (IMAGINE TONGUE–IMAGINE TOES∩MOVE TONGUE–MOVE TOES). The sections of the bilateral M1 (areas 4a and 4p), PMD (area 6), and the right putamen that were specifically active during imagery of tongue movement (see the text above) were also associated with the execution of tongue movements [as detected in the conjunction analysis, (IMAGINE TONGUE–IMAGINE FINGERS∩MOVE TONGUE–MOVE FINGERS), (IMAGINE TONGUE–IMAGINE TOES∩MOVE TONGUE–MOVE TOES)] (Table 1*c*).

Overlap of fMRI clusters and cytoarchitectural maps

In a purely descriptive approach, we *1*) computed the overlap of the fMRI clusters and the cytoarchitectural population maps of areas 4a, 4p, and 6; and *2*) related the location of the peak of the activations to the population maps (Fig. 3).

For the finger representation (Fig. 3, *a* and *b*) a cluster volume of 510 mm^3 was located in the left area 4a, 10 mm^3 in the left area 4p, and 1,620 mm^3 in the left area 6. The peak, located in the upper part of the anterior bank of the left central sulcus (x = −40, y = −28, z = 64), probably corresponded to area 4a (Fig. 3*b*; 40% of the postmortem brains). The peak, located on the left precentral gyrus (x = −32, y = −24, z = 68), corresponded to area 6 according to the cytoarchitectural population maps (30% of the brains had their area 6 represented at this site; see Fig. 3*a*). On the medial wall a finger-related peak was located just at the border between the most ventral part of SMA and the CMA (Fig. 3*c*).

At the level of the toes (Fig. 3*d*), 4,440 mm^3 of the cluster was located in the left area 4a, 340 mm^3 in the left area 4p, and 16,200 mm^3 in the left area 6 (Fig. 3*d*). The peak in the left paracentral lobule (x = −8, y = −28, z = 64) was located in the population map of area 4a (≥40% of the postmortem brains had their area 4a located at this site). The peak in the posterior part of the SMA (area 6; x = −8, y = −20, z = 72) corresponded to SMA (≥40% of the brains had area 6 represented here).

In the tongue zone (Fig. 3*e*), 3,480 mm^3 of the clusters was located in the left area 4a, 3,580 mm^3 in the right area 4a, 2,860 mm^3 in the left area 4p, 4,440 mm^3 in the right area 4p, 7,500 mm^3 in the left area 6, and 11,700 mm^3 in the right area 6 (Fig. 3*e*). Bilateral peaks were observed in area 6 (in ≥30% of the postmortem brains; see Table 1), and the central sulcus (x = −56, y = −12, z = 32; x = 56, y = −4, z = 32), corresponding to the border between areas 4a and 4p (areas 4a and 4p were both represented here in 30% of the brains).

Activations in individual subjects

In Table 2 we report the activations observed in individual subjects when we compared the different imagery conditions. In this purely descriptive approach, we report the BOLD signal increases in all subjects at the location of the peak voxels detected in the group analysis (taken from Table 1; see METHODS for details). For all subjects we inspected all 6 pairwise contrasts between the imagery conditions and they showed virtually the same results as those of the 3 main effects contrasts that are presented in Table 2. There were 2 important observations. First, all subjects displayed an increased level of activity at the sites that were found to be active in the group analysis ($P < 0.05$ uncorrected). In other words, the results obtained in the group analysis were consistent across all subjects. This rules out the possibility that the group results would have been biased by only one or a few of the subjects showing very strong effects (Friston et al. 1999). Second, when inspecting the activation maps from the individual subjects we observed activations of the tentative finger, toe, and tongue sections of M1: the cortex lining the anterior bank of the central sulcus (fingers and tongue) and paracentral lobule (toes; not shown). This observation rules out the unlikely possibility that the M1 activation observed in the group analysis could have been an artifact arising from the pooling of the data across individual subjects. In summary, the results form individual subjects corroborated the findings obtained in the group analysis.

DISCUSSION

In the present study we examined the brain activity when healthy subjects are imagining that they are making voluntary movements of their fingers, toes, and tongue. Our main results were obtained by contrasting these imagery conditions directly; these contrasts were matched in all aspects of all the tasks with the only difference being the body parts that the subjects were imagining that they were moving. Our results can thus be attributed directly to the body part in the motor image. The sections of the rostral part of the contralateral M1 (area 4a), the contralateral PMD (area 6), and the CMAc/SMA region that were associated with execution of finger movements were specifically active during the imagery of finger movements. Likewise, toe-related sections located in the posterior part of the SMA (area 6) and the contralateral M1 on the medial wall (area 4a) were more active during the imagery of toe movements than the imagery of the other body parts. Finally, the tongue regions of the left lateral premotor cortex (area 6) and bilateral M1 (areas 4a and 4p) were specifically activated while imagining making tongue movements. These results demonstrate that imagery of voluntary movement engages somatotopically organized sections of the primary motor cortex in a systematic manner and some body-part–specific region in the nonprimary motor areas. This finding provides support for the simulation hypothesis of motor imagery because it shows that imagery of different types of movement activates the relevant corresponding motor representations.

Because our experimental design depended on the capacity of the fMRI to detect anatomically distinct neural representations of the fingers, toes, and tongue, we will first briefly discuss the somatotopic maps obtained by contrasting the movement execution conditions. When the subjects executed the finger, toe, and tongue movements, we observed distinct activations associated with each body part in the M1, consistent with the known somatotopical organization of this area (Fig. 2; see further below). However, in the nonprimary motor areas we observed a more coarse somatotopical organization: in area 6 we detected different toe, finger, and tongue zones but the latter 2 were located in the lateral premotor cortex and the toe zone was located in the SMA. In the CMA, the only body-part–specific activation we detected was related to the finger movements. In other words, we found clear somatotopy in M1 but not complete somatotopical maps of the fingers, toes, and tongue within any nonprimary motor area as they are typically defined. Parenthetically, this could reflect the limited anatomical resolution of fMRI and the fact that the physiological activation of the nonprimary motor areas during performance of natural movements is not always strictly somatotopically organized (e.g., Ehrsson et al. 2000; Rintjes et al. 1999). However, the aim of the present study was not to address the issue of which of the nonprimary motor areas it is that contains a full representation of the body. The complete somatotopical organization of M1, the "gross" somatotopy of area 6, and the finger-specific zone in the CMAc provided us with sufficient information to answer our main question of whether imagery of the movement of different body parts would engage these areas in the same body-part–specific manner as movement execution.

To improve the anatomical localization of the activations we used cytoarchitectural maps from 10 postmortem brains (see METHODS for details). This technique provided us with an observer-independent possibility to define the most likely locations of areas 6, 4a, and 4p in the standard anatomical space. However, because of the limitations of this method some caution needs to be exercised when interpreting the results. First, there is a high degree of intersubject variability in the locations of the cytoarchitectural maps even after spatial normalization (e.g., Geyer et al. 2000; Roland et al. 1997). This means that a voxel in the standard anatomical space can correspond to different areas in different brains. Thus it cannot be excluded that a peak activation that was located in the population map of area 4a could in fact relate to activities in area 6 and area 4p in a few of the brains. Second, the population maps are based on a rather small number of microstructually mapped brains ($n = 10$). As a consequence, the exact location of the borders between the areas is somewhat uncertain. In short, the anatomical localization of activations in the cytoarchitectural areas should be considered as "strong indicators" and no more.

Motor imagery activates body-part–specific representations in the motor areas

The imagery of finger movements activated the left M1, the left PMD, and the CMAc/SMA region (Figs. 2 and 3). In the cluster on the left precentral gyrus and the central sulcus, one peak of activation was located on the crown of the precentral gyrus corresponding to the posterior part of area 6 and another peak was located on the anterior bank of the central sulcus belonging to area 4a. These sections of the PMD and the M1 correspond to finger representations as defined by the movement execution conditions in the present study and to the hand/finger zone as described in earlier human imaging studies (Ehrsson et al. 2000; Rijntjes et al. 1999). Likewise this location appears to correspond to a site that was previously reported to be active when humans imagine voluntary finger movements (Roth et al. 1995; Stephan et al. 1995). The finding that the cortices of the CMAc and the most ventral part of the SMA are active during imagery of finger action is consistent with the earlier observations that this CMAc/SMA region is active when subjects imagine that they are executing finger/hand movements compared with rest or nonimagery baseline conditions (Naito et al. 2002a; Stephan et al. 1995; Tyszka et al. 1994). This area also showed stronger activity during the execution of finger movements than toe or tongue movements, demonstrating that it corresponds to a hand representation (Fig. 2*f*). Indeed, this observation fits well with earlier human imaging and electrical stimulation studies (Deiber et al. 1999; Dettmers et al. 1995; Diehl et al. 2000; Ehrsson et al. 2001b; Fink et al. 1997; Mayer et al. 2001; Picard and Strick 1996; Stephan et al. 1995; Tyszka et al. 1994).

When the subjects imagined the toe movements we found activations located in the posterior part of the SMA and the M1 in the paracentral lobule (area 4a). These parts of the SMA and M1 corresponded to toe representations as defined by the movement execution conditions. Indeed, this region has previously been associated with movements of the lower right limb in human electrical stimulation (Fried et al. 1991; Hanakawa et al. 2001; Penfield 1951; Talaraich and Bancaud 1966) and functional imaging studies (Ehrsson et al. 2000; Fink et al. 1997; Mayer et al. 2001; Rijntjes et al. 1999).

The imagery of tongue movements most consistently activated parts of the bilateral PM and M1 (areas 4a and 4p) that were associated with overt tongue movements in the present study and that corresponded to the classical location of the tongue representation of the lateral frontal cortex (Fox et al. 2001; Penfield and Rasmussen 1952; Roland 1993b; Woolsey et al. 1952). In summary, these findings demonstrate that the pattern of somatotopical activation during motor imagery is very similar to the pattern observed during movement execution (see Figs. 2 and 3). Indeed, our results are consistent with the very recent fMRI study of Stippich et al. (2002) who investigated the activation of the precentral gyrus when subjects imagined movements of fingers, toes, and tongue and found evidence for a somatotopic activation pattern. However, our investigation provides several advantages compared with this latter study. First, we employed statistical parametric mapping to analyze the functional data form the whole cerebral cortex, whereas Stippich and colleagues (2002) studied only the region around the central sulcus. Second, in the present study we used cytoarchitectural population maps to localize the motor areas in a observer-independent way (they used arbitrarily criterions to define the primary motor cortex). Third, Stippich and colleagues (2002) contrasted only the activity registered during the imagery conditions with a resting baseline condition (with eyes open); they did not directly contrast the different motor imagery conditions (as we did). Thus it cannot be excluded that the activity they detected reflected general processes associated with imagery rather than the specific body part in the motor image. Nevertheless, the evidences currently available from the present investigation and the study of Stippich et al. (2002) strongly suggest that effector-dependent representations are recruited during movement imagination.

Motor imagery and M1 involvement

Interestingly, imagery of movement appeared to preferentially engage the cytoarchitectonic area 4a of the M1 (Fig. 3). The peaks of activation were located in area 4a during imagery of finger and toe movements and in the border-zone between area 4a and 4p when performing imagery of tongue movements (see RESULTS for details). Likewise, when we computed the volume of the active voxels that were located in the population map of areas 4a and 4p, we found that the volume of voxels located in area 4a was typically much larger than the volume in area 4p (see RESULTS). The involvement of 4a makes sense when one takes into account the fact that this rostral M1 field receives more extensive cortico-cortical projections from higher-order motor areas than area 4p, which in turn receives more input from somatosensory areas (see, e.g., Geyer et al. 1996; Porter and Lemon 1993; Strick and Preston 1982). Indeed, the motor cortical activation during motor imagery is believed to depend on top-down influences from higher-order frontal areas and our findings are compatible with this notion (Passingham 1997).

How can we reconcile our results with the fact that several earlier functional imaging studies failed to detect increases in activity in M1 when subjects imagined movement? We can think of at least 3 reasons: First, because the increases in synaptic activity in M1 are weak relative to the effects observed in the nonprimary motor areas (e.g., in the SMA) the failure to detect M1 activation could be a matter of limited sensitivity of the imaging technique used. Indeed, fMRI provides better statistical power than PET (because there is no limitation to the number of brain scans that can be acquired in each subject) and this could explain why PET studies have typically not detected activation of the precentral sulcus (but see Stephan et al. 1995), whereas several fMRI studies have done so (see INTRODUCTION). Indeed, recent studies using transcranial magnetic stimulation (TMS), which is a sensitive method with which to investigate the neuronal excitability of the motor cortex, have demonstrated increased excitability of the primary motor cortex during imagery of movement (e.g., Rossini et al. 1999). Second, without using cytoarchitectural population maps in the standard anatomical space, it is not possible to define the border between the M1 and the posterior part of area 6 in any neurobiologically meaningful way. Possibly, uncertainties about the area 4/6 border could have caused “mislocalization” of precentral activations. Third, the precise instruction to the subjects is important. In the present study subjects were explicitly instructed to imagine that they *voluntarily moved* their *own* body parts. The studies where the subjects imagined seeing their fingers moving (e.g., Decety et al. 1994; Deiber et al. 1998) did not record activation of the precentral gyrus, possibly because the subjects used visual imagery strategies.

Motor imagery: internal simulation of action

Our findings that imagery of the voluntary movement of a particular limb activates specific somatotopically organized motor representations provide support for the simulation hypothesis of motor imagery (Decety 1996; Jeannerod 1995; Jeannerod and Decety 1995; Jeannerod and Frak 1999). According to this hypothesis, the motor representations that are engaged when an action is executed are also recruited when the same action is imagined. Our results show exactly this: motor representations that are specifically involved in the control of the actual movement of a body part are activated when imagining the movement of the same body part and not during the imagination of movement of other body parts. Thus the brain appears to construct an internal simulation of the movement that the subjects are imagining that they are performing. This finding can explain the parallelism between imagery of action and actual performance of movements described in psychophysical studies (Parsons 1987, 1994; Sirigu et al. 1996). For example, the time it takes to imagine a movement depends on the body part and the posture of the limb (i.e., biomechanical and kinesthetic factors). Furthermore, the difficulty of imagining movements depends on the body part that the subjects are trying to imagine that they are moving (e.g., arm, leg, torso, head; Naito 1994). These psychophysical effects could be attributable to the differential activation of body-part–specific representations during the motor imagery because these representations are likely to encode the effector-dependent biomechanical and kinesthetic constraints of the imagined action.

In conclusion, we have demonstrated that motor imagery is associated with the activation of somatotopically organized sections of the motor cortices. Others have demonstrated a relationship between the specific type of visual stimuli being imagined and the activation of the corresponding stimulus-specific visual areas (Kosslyn et al. 1995, 1998; O’Craven and Kanwisher 2001). The present study extends this principle to the motor system: There is a direct relationship between the type of movement that is being imagined and the activation patterns of somatotopically organized motor areas.

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DISCLOSURES

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