Research report

Cortical and cerebellar activity of the human brain during imagined and executed unimanual and bimanual action sequences: a functional MRI study

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Abstract

The neural (blood oxygenation level dependent) correlates of executed and imagined finger sequences, both unimanual and bimanual, were studied in adult right-handed volunteers using functional magnetic resonance imaging (fMRI) of the entire brain. The finger to thumb opposition tasks each consisted of three conditions, two unimanual and one bimanual. Each experimental condition consisted of overt movement of the fingers in a prescribed sequence and imagery of the same task. An intricate network consisting of sensorimotor cortex, supplementary motor area (SMA), superior parietal lobule and cerebellum was identified when the tasks involved both planning and execution. During imagery alone, however, cerebellar activity was largely absent. This apparent decoupling of sensorimotor cortical and cerebellar areas during imagined movement sequences, suggests that cortico-cerebellar loops are engaged only when action sequences are both intended and realized. In line with recent models of motor control, the cerebellum may monitor cortical output and feed back corrective information to the motor cortex primarily during actual, not imagined, movements. Although parietal cortex activation occurred during both execution and imagery tasks, it was most consistently present during bimanual action sequences. The engagement of the superior parietal lobule appears to be related to the increased attention and memory resources associated, in the present instance, with coordinating difficult bimanual sequences.
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1. Introduction

Understanding the neural correlates of goal-directed action, whether executed or imagined, has been an important domain of cognitive brain research since the advent of functional imaging studies using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) [17,27–29,31,34,38,41]. A majority of studies has focused on the activation of individual brain areas, such as the sensorimotor cortex, the supplementary motor area (SMA) or the cerebellum. In this study, using fMRI of the entire brain, we aim to furnish a more complete view of brain activation during finger-sequencing tasks. We compare brain activation during overt and imagined movements, both unimanual (left and right hand separately) and bimanual (both hands sequencing together).

A complex movement task such as sequential finger movement involves many processes, including movement planning, selection, prediction and execution, whereas imagery of the same task requires the same set of processes, except the last. Due to this inherent difference in the nature of the two tasks, one should expect differences in brain activation. The question of whether motor execution and imagery share common neural resources has been addressed by many studies in the recent past.

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Significant increases in fMRI signal intensity were observed in the pre-central (primary motor cortex, M1) and the post-central gyri (primary somatosensory cortex, S1), during both motor performance and imagery of a finger-to-thumb opposition task [31]. The same task induced activation in contralateral M1, S1 and pre-motor cortices during actual execution but only in M1 and premotor cortex during mental simulation in another study [34]. When subjects were asked to make fists and then imagine doing the same, increased fMRI signal intensity was observed in M1, premotor cortex and the SMA during both execution and imagery tasks, with S1 showing significantly less activation during imagery [27]. Cerebral blood flow measured using PET was observed to increase in medial and lateral premotor areas as well as cingulate motor area (CMA) during both execution and imagery of joystick movements [38]. The latter study also reported additional activation in primary sensorimotor cortex and rostral superior parietal lobe during task execution [38]. Compared to actual motor performance, imagery appears to produce significantly lower fMRI signal changes in the cerebellum [27,28]. Although these studies used different tasks (making fists [27] and finger to thumb opposition [28]), both reported differential activation of the cerebellum during execution and imagery: strong activation of the anterior cerebellum was observed during execution while imagery resulted in posterior lobe activation. Movement execution thus seems to engage a large network of brain areas including the M1, S1, premotor areas (SMA, CMA), superior parietal lobule and the cerebellum. Imagery of the same movements seems to engage almost all these areas, although the intensity of activation appears to drop off in S1 and cerebellum.

Unimanual and bimanual tasks employ overlapping as well as different neural resources [13]. In right-handed individuals, the right sensorimotor cortex was found to be more active than the left in unimanual finger sequencing tasks, whereas the left showed more activation than the right sensorimotor cortex during bimanual tasks [13]. For both unimanual and bimanual tasks, the area and intensity of brain activation appear to increase with task complexity, force and rate of movement [13,14,32,33,35,36,40,42]. SMA, pre-SMA and CMA have been implicated in the control of complex finger movements [5,6,15,25,36]. Comparing repetitive tapping of the index finger with sequential movement of fingers, Wexler et al. [42], found that the parietal lobe, especially the superior parietal area, was selectively activated in the more complex finger-sequencing task. In self-paced finger movements, however, cortical structures around the intra-parietal sulcus were activated [35]. The intra-parietal sulcus is also active when finger movements are coordinated with reference to a specific spatial reference [1,16]. It appears that the parietal cortex is involved in a wide variety of tasks, especially those in which subjects need to access spatial information and spatial memory. Since unimanual and bimanual tasks

basically differ in the involvement of one versus two hemispheres, studies have focused on the laterality of brain activation during such tasks. In right-handed individuals, significant ipsilateral (left) motor cortex (M1) activation is observed during movement with the non-preferred (left) hand [25,37]. Such ipsilateral activation for movement of the non-dominant hand has been attributed to task complexity [33]. Similarly, some studies have reported bilateral cerebellar activation when right-handed subjects moved using their non-dominant left hand [8,14]. These findings suggest that when subjects perform tasks with their non-dominant hand, an additional neural loop consisting of motor areas of both the hemispheres is involved, that facilitates coordination of motor behavior.

In the present study, we aim to identify the brain areas involved in both overt finger sequencing and imagery alone conditions. Following Jäncke et al. [13] we studied differences in brain activation between unimanual and bimanual finger movements. Here, however, instead of using a simple finger-sequencing (2345) task, a different movement sequence was prescribed for each task (left, right and bimanual conditions) in order to minimize or at least balance effects due to learning, and to control for task difficulty across exemplars of the task. By imaging the entire brain during these tasks, our main goals were 2-fold: first, to understand how cortical and cerebellar areas are differentially engaged during the course of motor performance and imagery. In particular, we expected on the basis of older [22] and more recent models of motor control [43] which posit extensive internal feedback and feedforward cerebro-cerebellar loops, that cerebellar involvement will be greater during active, planned than imagined movement sequences. This is because of the putative role of the cerebellum in correcting errors in motor commands prior to their effects at the periphery. Our second goal was to clarify the role of parietal and other cortical areas in movements such as complex bimanual action sequences, which incorporate spatial information and spatial memory. In particular, evidence from patients with parietal lesions suggests frank motor imagery deficits [4,18]. On this basis, we might expect greater parietal involvement as the task becomes more difficult to imagine, such as when the non-preferred hand is used or when both hands are sequencing together.

2. Materials and methods

2.1. Subjects

In this study eight healthy right-handed volunteers participated, three males and five females, aged 25–40 years. Informed consent was obtained from all subjects. Handedness was determined by simple inquiry, consisting of a few questions from the Edinburgh Handedness Inventory. All subjects were neurologically intact. No one

reported any psychiatric or cardiovascular illness and none were on medication.

2.2. Task

The experiment consisted of three conditions, two unimanual and one bimanual. During the unimanual condition, subjects performed movements with the right or left hand alone, whereas the bimanual task was carried out using both hands simultaneously. During the experiment, the hands were kept in a semi-prone position, by the subject's side, so that the experimenters were able to see the subject's finger movements at all times (and lack of such during imagery conditions). The fingers were labeled 1–5 from the thumb to the little finger (anatomical convention) and the sequences were 5342, 2435 and 4253 for left, right and bimanual conditions, respectively. Task instructions were given to subjects just before the beginning of each experimental condition. Subjects were asked to keep their eyes closed during the entire experiment and to concentrate on the task, opposing thumb to fingers as fast, firmly and accurately as possible. Subjects were monitored throughout the experiment for movement speed and precision. Each experimental condition consisted of overt movement of the fingers in a prescribed sequence and imagery of the same task. For the latter, subjects were instructed to imagine making the requested finger sequences as quickly and as accurately as possible, and to remain relaxed without moving their fingers. The order of conditions was randomized across subjects.

2.3. Image acquisition protocol

Whole brain fMRI data acquisition was carried out using a 1.5-Tesla Signa scanner (General Electric Medical Systems, Milwaukee, WI), equipped with echo planar imaging (EPI) capabilities. Images were acquired with the participants lying supine inside the scanner. Before entering the scanner, subjects were briefed about the tasks to be performed. The sequence of finger movements was explained to them when they were inside the scanner. Each condition (unimanual and bimanual) lasted for 4 min, and was comprised of four periods of activation (ON, task) during which subjects performed the task and four baseline (OFF, rest) periods in which subjects heard only the ambient machine noise. Alternating periods of task and rest were cued to the subject through instructions to 'move' and 'rest', respectively, delivered through a microphone. The two phases of each condition: overt movement (right, left and bimanual) and imagery (right, left and bimanual) lasted 12 min each. Throughout the experiment, the subject's head was supported by a comfortable foam mold. Head movement was further minimized using foam padding and forehead restraining straps.

Scanning started with the acquisition of full head, 3D SPGR (spoiled gradient) anatomical images, with the following imaging parameters: field of view (FOV)=26 cm, frequency–phase matrix=256×256, repetition time (T_R)=34 ms, echo time (T_E)=5 ms, flip angle (FA)=45°, slice thickness 2 mm, and one excitation per phase encoding step. For each subject, T2*-weighted gradient echo, echo planar multi-slice datasets were acquired during performance of the finger sequencing tasks (T_R=3000 ms; T_E=60 ms; FA=90°; 20 axial slices, frequency–phase matrix=64×64; FOV=24 cm; slice thickness=5 mm and inter-slice gap=2.5 mm). Thus the voxel size was 3.75× 3.75×7.5 mm. High-resolution background images (same 20 slices, frequency–phase matrix size=512×512) were also acquired for overlaying the functional data.

2.4. Data analysis

The software packages used for data analysis were AFNI (Analysis of Functional NeuroImages, Medical College of Wisconsin [2]) for display and analysis, and SPM (Statistical Parametric Mapping, Wellcome Department of Cognitive Neurology, London) for coregistration. For each subject the following steps of analysis were performed:

(1) Movement correction of the functional datasets using the Fourier method in AFNI [3].
(2) Cross-correlation with a boxcar reference function (30 s on, 30 s off) which was shifted by 6 s to account for the delay of the hemodynamic response. This shift was determined by examining the raw time series data. AFNI creates a dataset, which contains two numbers per voxel representing the cross-correlation value (a number between −1 and 1) and the intensity.
(3) Masking out all voxels with a cross-correlation (with zero-time lag) of smaller than 0.5 leads to datasets of intensities for active voxels only.
(4) Coregistration and reslicing of the high-resolution background images and the intensity dataset with a full-head T1-weighted scan with cubic voxels of 2 mm (done in SPM).
(5) Transformation into Talairach stereotaxic space [39].
(6) Identification of clusters of active voxels using cluster size thresholding. The minimum volume for a cluster was determined using the AlphaSim module in AFNI. This procedure uses Monte Carlo simulations to create random datasets in order to determine the probability of finding activations due to chance. With the underlying assumption that such activity is more likely in single voxels than clusters of voxels, probability values are calculated for clusters with different volumes and active voxels within a certain distance [44]. In our case, these values turned out to be 4 mm for the distance between active voxels and a volume of 40 μl in order to achieve an overall significance of $P<0.01$.

In individual subjects, brain areas with active clusters were identified by their coordinates in Talairach stereotaxic space using the 'Talairach daemon', a web-based interactive program that reads out the brain area when the coordinates of a voxel are given [26]. Once clusters were identified in the individual data (for every condition and every subject) these data were subjected to a two-way analysis of variance (ANOVA) using 'hand' (three levels: left, right, bimanual) and 'state' (two levels: movement and imagery) as the two crossed factors. Significant voxels were overlaid in color over the anatomy with positive activations, i.e., higher MR signal amplitude during task compared to rest, ranging from red (minimum) to yellow

(maximum) and negative activations ranging from blue to cyan.

3. Results

All subjects performed the task sequences correctly at movement rates that were quite similar across subjects. No overt movement was observed during the imagery tasks. During post-experiment interviews in which subjects were asked to evaluate their performance, some subjects reported that imagining bimanual sequences was the most difficult task.
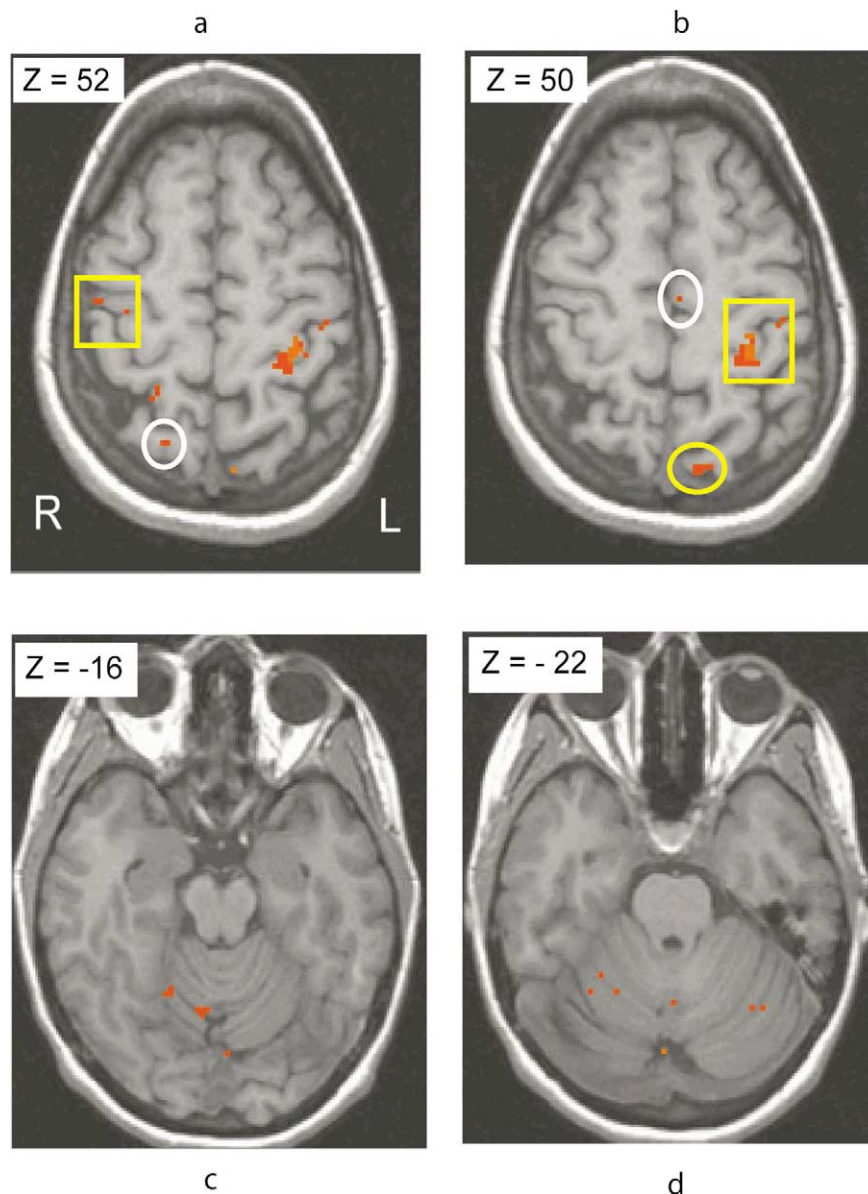

Fig. 1. Comparison of bimanual versus left-handed execution of finger sequences yielded significantly greater activity ($P<0.01$) in the right pre-central gyrus (square, a), right precuneus (oval, a), left sensorimotor cortex (square, b), left precuneus (yellow oval, b), SMA (white oval, b), and bilateral cerebellum (colored voxels, c,d). Activity is overlaid on a representative individual brain. The Z values show the slice position along the vertical axis in the Talairach coordinate system. R and L indicate the right and the left side, respectively.
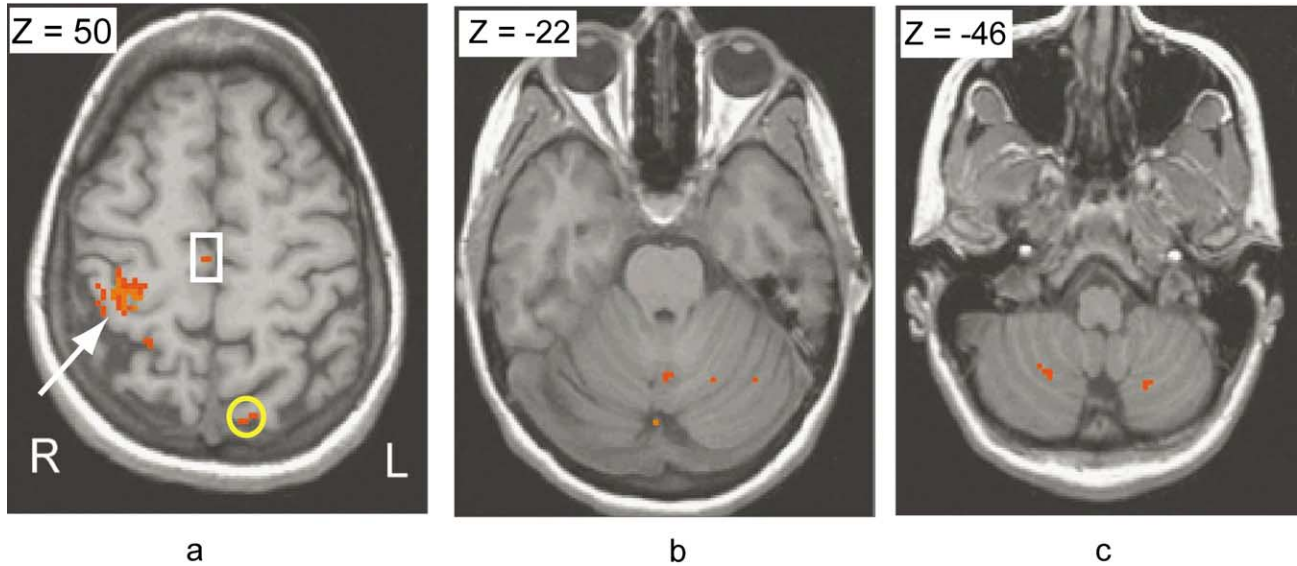
Fig. 2. Comparison of bimanual versus right-handed execution of finger sequences yielded significant voxels (*P*<0.01) in the left precuneus (yellow ellipse, a), right sensorimotor cortex (arrow, a), SMA (rectangle, a) and bilateral cerebellum (colored voxels, c,d). Greater activity (voxels in red) is observed during bimanual than right-handed action sequences. The *Z* values show the slice position along the vertical axis in the Talairach coordinate system. R and L denote the right and the left side, respectively.

3.1. Group analysis

ANOVA revealed a main 'hand' effect ($F(2,42)=5.14$; at $P<0.01$) in bilateral pre- and post-central gyri. Similarly, a main effect of 'state' ($F(1,42)=7.28$; $P<0.01$) was also found in bilateral pre- and post-central gyri, SMA,
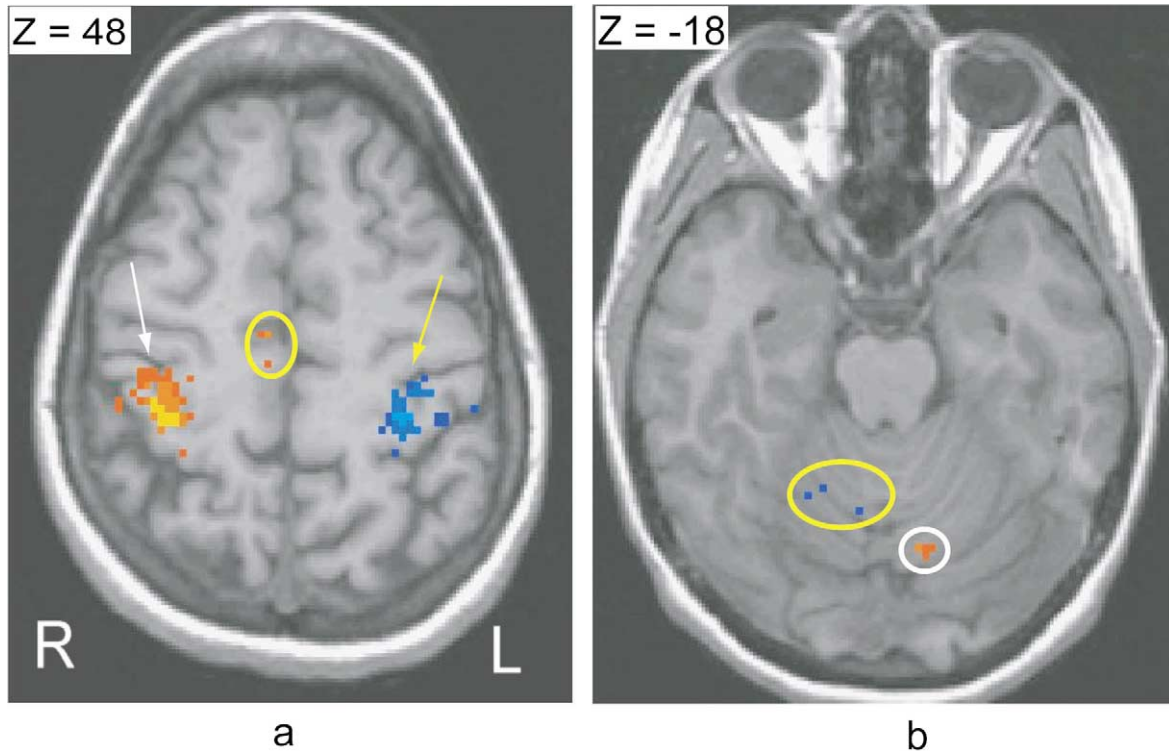

Fig. 3. Comparison of left versus right-handed execution tasks. The right sensorimotor cortex (white arrow, a), SMA (yellow oval, a) and the left cerebellum (white oval, b) have more activation during left-handed than right-handed execution and the left sensorimotor cortex (yellow arrow, a) and right cerebellum (yellow oval, b) show more activity during right hand execution. The *Z* values show the slice position along the vertical axis in the Talairach coordinate system. R and L denote the right and the left side, respectively.

bilateral parietal lobe, bilateral precuneus and bilateral cerebellum. The interaction ($F(2,42)$) between hand and state was also significant ($P<0.01$). In the following, we unpack this interaction using conservative ($P<0.01$) post-hoc *t*-tests.

3.1.1. Execution

3.1.1.1. Bimanual versus unimanual. Post-hoc analysis revealed greater activity for bimanual than left-handed movements in the left sensorimotor cortex, bilateral superior parietal lobules, supplementary motor area (SMA) and bilateral cerebellum. Fig. 1a shows enhanced activity in the right precuneus and the right precentral gyrus, Fig. 1b shows increased activity in the left sensorimotor area, SMA and the left precuneus, and Fig. 1c,d depicts greater activity in bilateral cerebellum during bimanual action sequences.

Significant differences ($P<0.01$) were also found between bimanual and right-handed finger movements in the right sensorimotor cortex, SMA, left precuneus, and bilateral cerebellum. Fig. 2a shows enhanced activity in the right sensorimotor cortex, SMA and left precuneus. Fig. 2b,c shows higher intensity activation in bilateral cerebellum during bimanual action sequences.

3.1.1.2. Unimanual differences: left versus right. A comparison of left and right-handed movement sequences revealed significant ($P<0.01$) voxels in right sensorimotor cortex, SMA and left cerebellum (and corresponding negative differences in the left sensorimotor cortex and right cerebellum). The red and yellow voxels in Fig. 3a show enhanced activity in the right sensorimotor cortex and SMA during left-handed action sequences, while the blue voxels depict enhanced activity in the left sensorimotor cortex during right-handed action sequences. Fig. 3b shows enhanced activity in the left, ipsilateral cerebellum (red voxels) during the left-handed sequencing task and also in the right cerebellum during the right-handed task (blue voxels).

3.1.2. Imagery versus execution

Comparison of left-handed execution and imagery tasks revealed significantly active voxels ($P<0.01$) in the right sensorimotor cortex, SMA, and the left cerebellum (Fig. 4). The colored voxels in Fig. 4 depict enhanced activity in SMA, right sensorimotor cortex (Fig. 4a) and left cerebellum (Fig. 4b) during left-handed execution. A similar comparison between executed and imagined right-handed sequences revealed significantly active voxels in the left sensorimotor cortex, left superior parietal lobule (Fig. 5a) and the right cerebellum (Fig. 5b). Significant differences
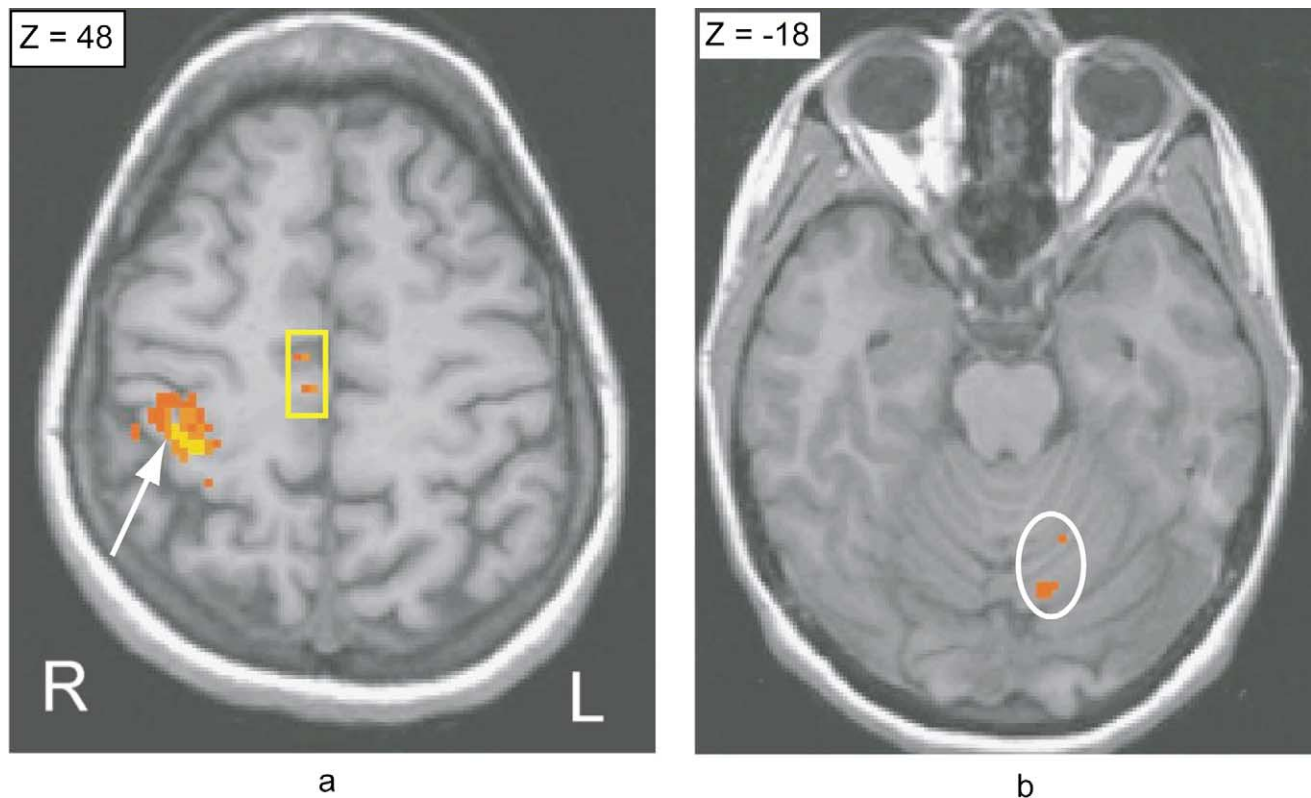

Fig. 4. Comparison of left-handed execution versus left-handed imagined tasks. Significantly greater activation ($P<0.01$) was observed in the right sensorimotor cortex (arrow, a), SMA (rectangle, a), and the left cerebellum (white oval, b) during execution. The Z values show the slice position along the vertical axis in the Talairach coordinate system. R and L denote the right and the left side, respectively.
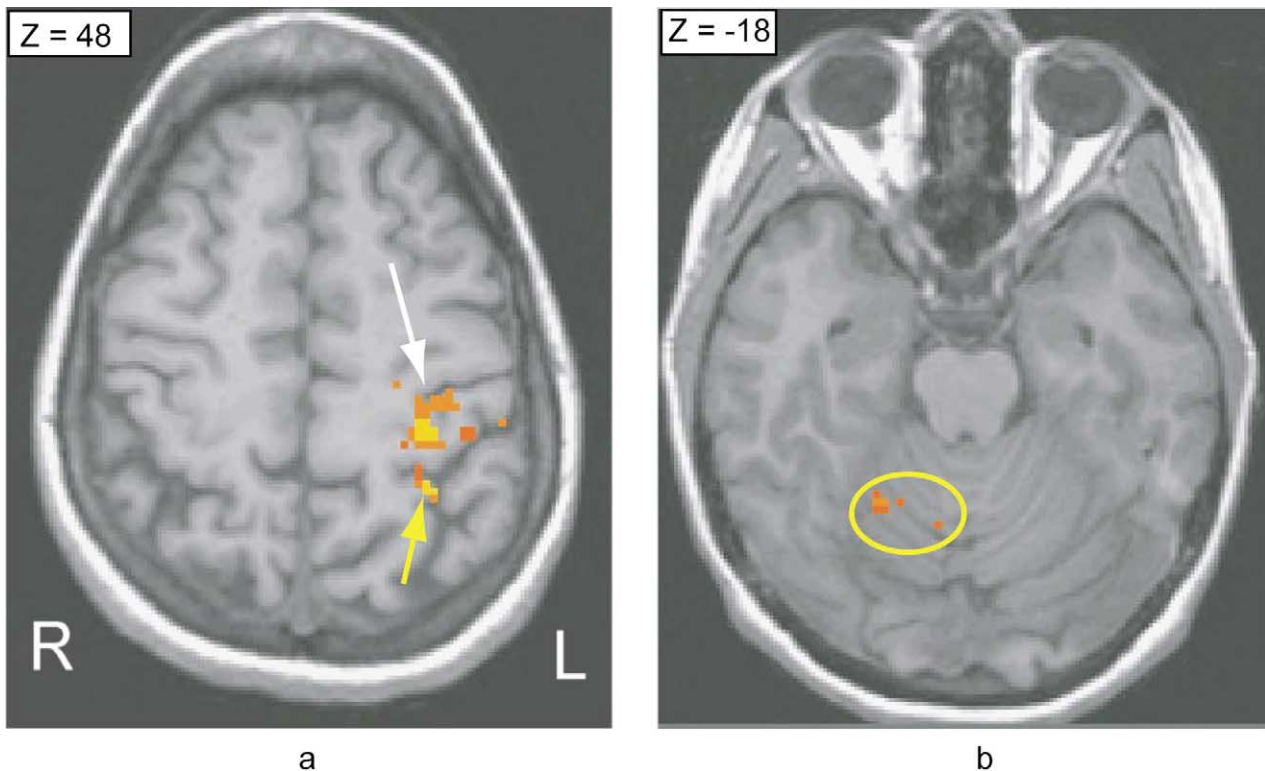
Fig. 5. Comparison of right-handed execution versus right-handed imagery shows significant differences ($P<0.01$) in the left sensorimotor cortex (white arrow, a), left superior parietal lobe (yellow arrow, a) and the right cerebellum (oval, b) indicating greater activation during execution. The Z values show the slice position along the vertical axis in the Talairach coordinate system. R and L denote right and left, respectively.

between bimanual execution and bimanual imagination tasks were observed in bilateral sensorimotor cortices, bilateral precuneus, SMA, bilateral inferior parietal lobules, and bilateral cerebellum (Fig. 6). Enhanced activity in bilateral sensorimotor cortices and SMA can be seen in Fig. 6a,b, right precuneus in Fig. 6a, left precuneus activity in Fig. 6b, bilateral inferior parietal lobules in Fig. 6c, and bilateral cerebellum in Fig. 6d.

3.2. Individual analysis

Variability in brain activation is to be expected among subjects. Fig. 7 provides an 'activation grid' which depicts brain activation (hatched regions) in our subjects during the six tasks. The top row of the figure shows activity during the three execution tasks (left, right and bimanual) and the bottom, activation during imagery tasks. The numbers on the Y-axis represent individual subjects 1–8; RM and LM, right and left primary motor area; RS and LS, right and left primary somatosensory area; SM, supplementary motor area; RP and LP, right and left superior parietal lobule; RC and LC, right and left cerebellum. It can be seen that cerebellar activity (last two columns) in most of the subjects drops off during the imagery tasks. Subjects show maximum activation during the bimanual execution task (top right).

Clusters of brain areas active for all subjects during

execution and imagery conditions were tabulated to examine similarities in patterns of neural activation. Table 1 gives the number of subjects with activation in different brain areas during all six tasks. The rows depict individual brain areas and the six columns represent the six tasks. Two asterisks indicate seven or more subjects, a single asterisk indicates four to six subjects and a blank cell indicates that only three or fewer subjects showed activation in that particular brain area. Maximum activation was seen in all areas during the bimanual execution task (fifth column). There is more ipsilateral activation in the sensorimotor cortex during the left (non-preferred hand) movement task than the right-handed (preferred hand) movement task (compare columns 1 and 3). A general reduction in activity was observed during the imagery tasks, especially in the somatosensory cortex and the cerebellum (columns 2, 4 and 6). SMA was consistently active during both movement and imagery tasks (row 3), whereas activity in the cerebellum dropped off markedly during the imagery tasks (compare data in columns 1 and 2, columns 3 and 4, columns 5 and 6).

4. Discussion

Given the complexity of voluntary movement, both in terms of the selective engagement of neuroanatomical
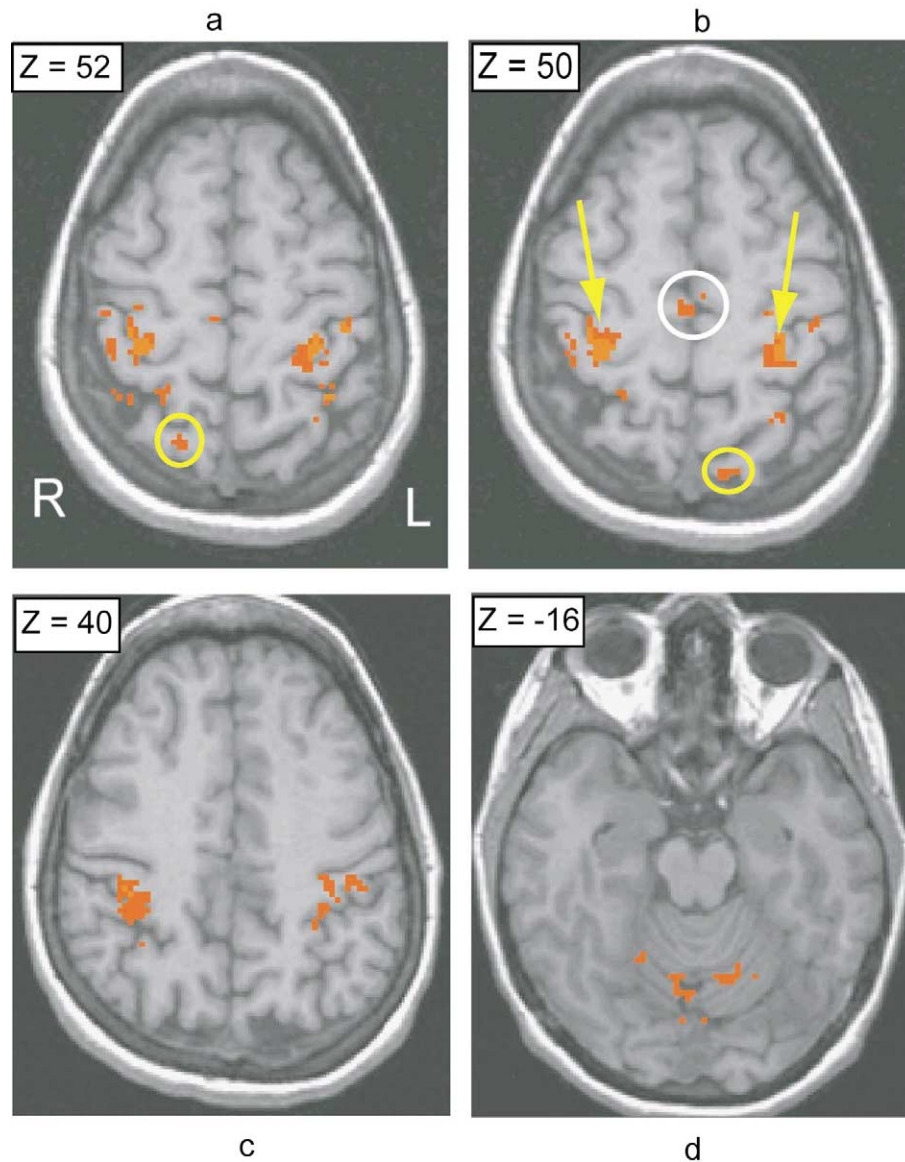
Fig. 6. Comparison of bimanually executed and imagined action sequences resulted in greater activation in right precuneus (yellow oval, a) bilateral sensorimotor cortices (yellow arrows, b), SMA (white oval, b), left precuneus (yellow oval, b), bilateral parietal lobes (c), and bilateral cerebellum (d) during the bimanual execution task. The Z values show the slice position along the vertical axis in the Talairach coordinate system. R and L denote the right and the left side, respectively.

structures in time and the vast repertoire of behaviors possible, it is reasonable to assume that an intricate network of cortical and subcortical structures is involved, especially in fine movements such as finger sequencing. Definitive answers are clouded, however, by the wide variety of tasks employed and because the same set of task components is seldom studied in the same subjects. Two important points may be gleaned from the diverse activations observed in different studies: (i) the brain activation observed depends largely on the nature of the task; and (ii) seemingly complex tasks require the recruitment of a larger and more intricately connected network of brain areas.

A key feature of the present experimental design was

that the same subjects were examined in a spatiotemporal sequencing task that isolated the dimensions of handedness (left and right), manual engagement (unimanual and bimanual) and cognitive influences (imagined and executed) on action. Overall effects of these manipulations are present in the brain, as well as interesting differences among individuals in the way neural areas are engaged and disengaged in sequential tasks.

As expected, activation in cortical and cerebellar regions of the brain is associated with the planning and execution of spatiotemporal actions. Pre- and post-central gyri, SMA, parietal cortex and cerebellum are all recruited to differing degrees in active, self-generated action sequences. These regions are certainly necessary, if not sufficient, for this
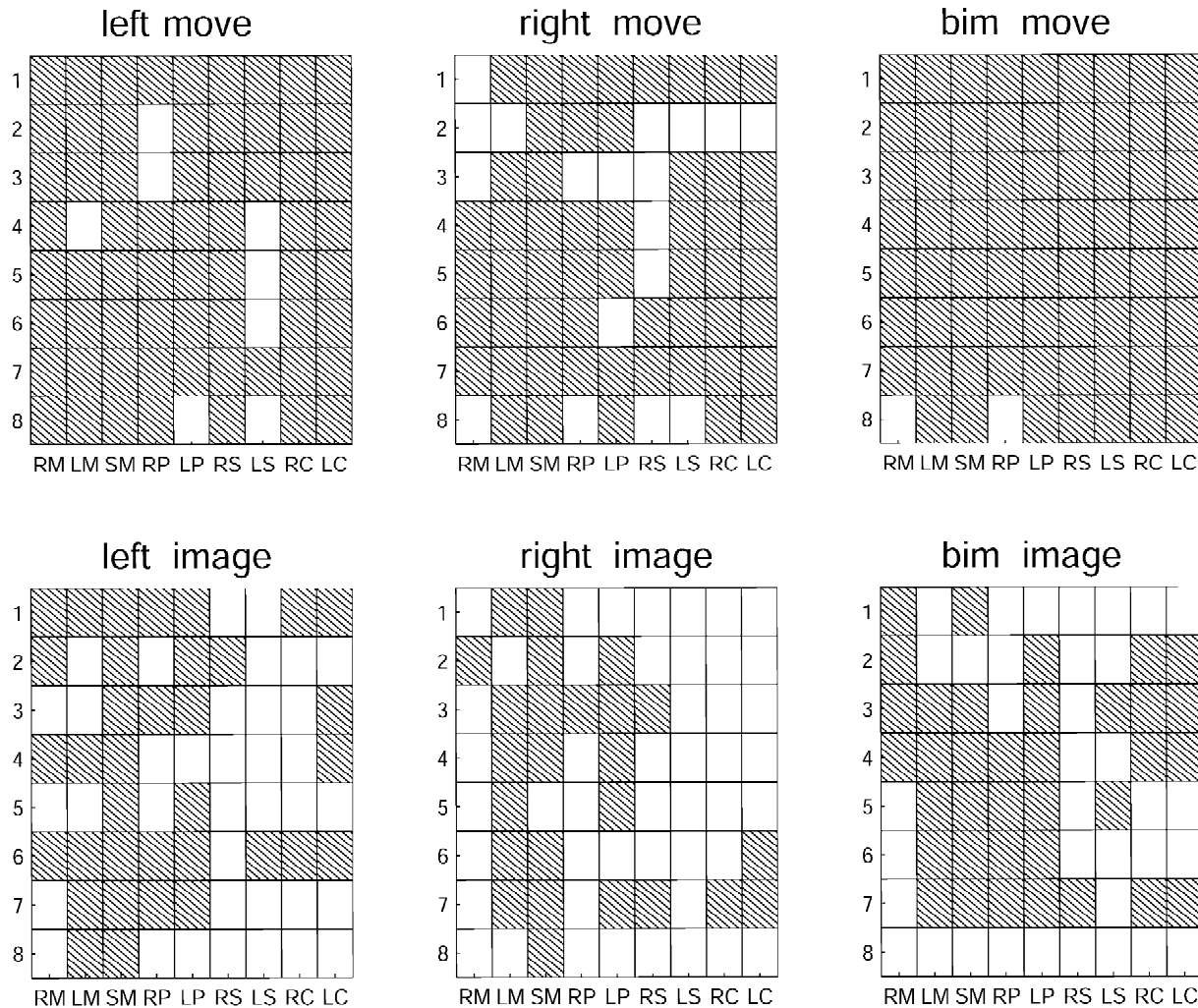
Fig. 7. shows an 'activation grid' which depicts brain activation (hatched regions) of all subjects during the six tasks. The top row shows activity during the three execution tasks, left, right and bimanual (indicated by left-move, right-move and bim-move, respectively). The bottom row shows activity during imagery tasks (indicated by left-image, right-image and bim-image). The numbers on the Y-axis represent individual subjects 1–8. R and L on the X-axis denote the right and left hemispheres; M, primary motor area; S, primary somatosensory area; SM, supplementary motor area; P, superior parietal lobule; C, cerebellum.

kind of task. Examination of individual data revealed that bilateral primary motor cortex was activated more prominently when the task was performed with the non-preferred left hand (Fig. 7 and Table 1). This, along with the fact that ipsilateral motor cortical activation was greater in the left hand, suggests that subjects' reported difficulty in performing action sequences lies at the executional level. Notably, SMA is similarly engaged in all movement conditions, in all subjects.

An interesting finding was that the superior parietal lobules are involved especially, though not uniquely, in coordinating bimanual sequences. It is reasonable to assume, in accordance with our subjects' verbal reports, that bimanual sequential actions place greater demands on attention and memory, as well as execution. A considerable amount of evidence implicates parietal cortex in the execution of hand movements [4]. Relatedly, our results

showing that parietal cortex is significantly more active in bimanual and left-handed execution relative to imagery conditions, suggest a connection between parietal cortex and task difficulty [42]. In both execution and imagery tasks, subjects had their eyes closed and hence had to rely on knowledge of the spatial dimensions of the task along with the sensory feedback that they experienced during movement. Accessing this memorized spatial information may result in the precuneus activation observed in our subjects during execution and imagery.

Imagining and performing coordinated movements engage SMA and superior parietal cortex to varying degrees. Only in actually performed action sequences are precentral, post-central and cerebellar cortices active. These results taken in tandem suggest that both unimanual and bimanual actions involve a distributed network that, at the very least, engages all these areas. The actual time-depen-

Table 1
Activation in different brain areas during different tasks

Brain area	Lt move	Lt image	Rt move	Rt image	Bi move	Bi image
R. M1	**	*	*		**	*
L. M1	**	*	**	*	**	*
SMA	**	**	**	**	**	*
R. S1	**		*		**	
L. S1	*		*		**	
R. SPL	*	*	*		**	*
L. SPL	**	*	*	*	**	*
R. Cll	**		**		**	*
L. Cll	**	*	**		**	*

This table shows the number of subjects with activation in different brain areas during the six tasks. The letters L and R indicate left and right hemisphere, respectively. M1, primary motor area; SMA, supplementary motor area; S1, primary somatosensory area; SPL, superior parietal lobule; Cll, cerebellum. The following schematic representation is used to denote the number of subjects showing activation in a brain area: three or less by blank; four to six by an asterisk (*); and seven or more by two asterisks (**).

dence of this process cannot be assessed using fMRI alone. However, in conjunction with multi-channel MEG and EEG recordings, deeper insights into the spatiotemporal dynamics of the human brain may well emerge [20]. In light of previous evidence it seems likely that SMA is involved in the planning and preparation of action sequences whether real or imagined. Parietal cortex (especially the superior parietal lobule, Brodmann's area 7, the precuneus) is engaged most especially for bimanual action sequences that rely on remembering and executing the correct ordering of task components along with processing the sensory consequences of action.

A key result is that sensorimotor cortical and cerebellar areas appear to be functionally decoupled from the task network when people imagine but do not actually execute sequential actions. The suppression of activity in these areas and their corresponding activation during normal movement suggests the involvement of a cerebro-cerebellar internal feedback loop. From clinical studies, the latter has long been implicated in the initiation and control of voluntary movement. The crucial idea is that feedback is generated internally ('corollary discharge') not only from peripheral receptors as a consequence of muscular contraction [10,22]. Long ago, Oscarsson [30] identified a functional role for interneuronal pools that carry specific information from descending motor paths. His work on the functional organization of spino- and cuneocerebellar tracts promoted the hypothesis that the anterior lobe of the cerebellum is important for correcting 'errors' in motor activity elicited from the cerebral cortex. The cerebellum was seen as receiving information about command signals from the motor cortex, the effects these signals evoke on lower motor areas that are also influenced by peripheral afferents, and the evolution of action as conveyed by extero- and proprioception. Massive interconnectivity between cerebral cortex and cerebellum led Ito [12] to

propose that cerebellum monitors cortical output and feeds back corrective information well before cortical output gives rise to activity in motor neurons. Resulting sensory information may then act to stabilize movement via afferent feedback connections to the post-central cortex [23]. Such notions figure prominently in modern computational models of motor control, which posit a role for 'internal modeling', as a way to circumvent peripheral delays once movements are highly practiced [22,43]. Our data suggest rather strongly that only intended and realized action sequences engage this hypothesized cortico-cerebellar loop. Sans actual movement there is little or no observed cerebellar activity, whether in control signals from motor cortex or as a result of information processing in post central receiving areas.

It is clear from the present work that the brain engages multiple cortical and cerebellar structures to varying degrees for planned sequential action. More and more evidence points to the brain as a highly interconnected, spatiotemporal dynamical system that uses distributed representational schemes [7,9,11,19,21]. This means that any particular cognitive task is likely to engage (and disengage over the course of time) multiple brain regions in a task-specific fashion. In this respect, more work, both conceptual and empirical, needs to be done on a 'theory of tasks': which task components are shared by particular brain regions and which are unique to particular exemplars of a given task. It may be that this effort will be facilitated by the theory of coordination dynamics [11,21,23,24], which displays certain universal properties (e.g., multiple steady states, transitions, metastability, etc.) that are common across different task realizations.

Acknowledgements

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