

Zones of bimanual and unimanual preference within human primary sensorimotor cortex during object manipulation

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We asked which brain areas are engaged in the coordination of our hands in dexterous object manipulations where they cooperate for achieving a common goal. Well-trained right-handers steered a cursor on a screen to hit successively displayed targets by applying isometric forces and torques to a rigid tool. In two bimanual conditions, the object was held freely in the air and the hands thus generated coupled opposing forces. Yet, depending on the mapping rule linking hand forces and cursor movements, all subjects selected either the left or the right hand as prime actor. In two unimanual conditions, the subjects performed the same task with either the left or the right hand operating on a fixed tool. Functional magnetic resonance imaging revealed common activation across all four conditions in a dorsal fronto-parietal network biased to the left hemisphere and in bilateral occipitotemporal cortex. Contrary to the notion that medial wall premotor areas are especially active in complex bimanual actions, their activation depended on acting hand (left, right) rather than on grip type (bimanual, unimanual). We observed effects of grip type only in the primary sensorimotor cortex (SMC). In particular, with either hand as prime actor, bimanual actions preferentially activated subregions of the SMC contralateral to the acting hand. A sizeable subregion with preference for unimanual activity was found only in the left SMC in our right-handed subjects. Collectively, these results indicate a hemispheric asymmetry for the SMC and that partially different neural populations support the control of bimanual versus unimanual object manipulations.

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Introduction

Most previous researches on cerebral control of bimanual actions have addressed situations where the two hands simultaneously perform independent tasks, typically involving finger tapping or other gestures

(see Swinnen, 2002; Wiesendanger and Serrien, 2004 for reviews). Mesial wall premotor areas (supplementary and cingulate motor areas) together with lateral premotor areas, parietal cortex and cerebellum typically show higher or more extensive activation during bimanual as compared to unimanual movements (Goerres et al., 1998; Jäncke et al., 1998; Tracy et al., 2001; Toyokura et al., 2002; Nair et al., 2003; Debaere et al., 2004). Furthermore, these brain regions tend to be more engaged during asymmetric or out-of-phase bimanual movements than in mirror-symmetric or in-phase movements (Sadato et al., 1997; Goerres et al., 1998; Stephan et al., 1999a,b; Toyokura et al., 1999; Immisch et al., 2001; Serrien et al., 2001; Meyer-Lindenberg et al., 2002; Ullén et al., 2003; Debaere et al., 2004; Wenderoth et al., 2005). Given that the hands have greater difficulties acting independently under asymmetric gestures (Swinnen, 2002), this increase in brain activity is thought to reflect an ‘additional coordination effort’ required to overcome difficulties in interhemispheric spatiotemporal integration (Debaere et al., 2004; Wenderoth et al., 2005). Natural object-oriented bimanual activities, however, run apparently effortlessly although they commonly involve coordinated action patterns with complex mixtures of mirror-symmetric and asymmetric components. In such activities, the two hands are functionally bound together in time and space for attaining a common goal, such as when opening bottles and jars, buttoning a shirt and playing a violin. Thus, rather than simultaneously performing separate tasks, the hands play complementary roles where one in each instance serves as prime actor while the other has a stabilizing or assisting function (Guiard, 1987; MacNeilage, 1987; Viallet et al., 1992; Johansson et al., 2006).

To learn about neural mechanisms that support bimanual coordination during object manipulations, we used functional magnetic resonance imaging (fMRI) to compare brain activity while well-trained right-handers completed the same task under comparable bimanual and unimanual conditions. In the bimanual conditions, the subjects applied longitudinal and twist forces to a tool held freely between the hands to control a cursor for hitting targets on a computer screen. Based on converging evidence from correlations between applied forces and tool movements, neurophysiological (electromyography, transcranial magnetic brain stimulation) and fMRI data, we have previously demonstrated that the brain in such situations flexibly assigns as prime actor the hand (left or right) whose forces are directionally most spatially congruent with the

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movement goal (Johansson et al., 2006). The accompanying hand, bound to generate forces directed opposite to the goal motion, is assigned an assisting, or postural, role. By applying different mapping rules between hand forces and cursor movements, we created two bimanual conditions where either the left or the right hand functioned as prime actor. In both condition, the two hands generated complex combinations of coordinated mirror-symmetric and anti-symmetric actions. In the unimanual conditions, the tool was fixated and the subjects performed the same task by applying forces by either the left or the right hand. The forces generated by a single hand were virtually identical to those applied by the same hand in the bimanual conditions. In a factorial analysis, we examined the effect of grip type (unimanual, bimanual) and acting hand (left, right) on blood oxygen level-dependent (BOLD) signals recorded from the whole brain as well as possible interaction effects between these factors. Our results, based on object manipulation, challenge the generality of the notion that tasks requiring complex coordinated bimanual actions employ more neural resources than used when the corresponding action components are performed unimanually. For premotor areas, our results suggest that their engagement rather depends on primarily acting hand (left or right) than on whether a task is performed unimanually or bimanually. Finally, we submit that the control of bimanual and unimanual object manipulations use partially different hand representations in the primary sensorimotor cortex.

Materials and methods

The present results are based on the same brain scanning experiment as reported on in a previous study that concerned hand assignments in the bimanual conditions (Johansson et al., 2006).

Subjects, general procedure and apparatus

Sixteen right-handed (Oldfield, 1971) humans (8 males and 8 females) ranging from 23 to 37 years of age participated after providing written informed consent in accordance with the Declaration of Helsinki. Their task was to move a cursor (filled circle, 0.2° visual angle) on a computer screen in order to hit, as fast as possible, successively displayed targets (open square, 0.8° visual angle) (Fig. 1A). They moved the cursor by applying forces either bimanually or unimanually to cylindrical handles (diameter = 3.4 cm, length = 3 cm) attached to each side of a rectangular box ($12 \times 8 \times 3.5$ cm) (Fig. 1B). In the unimanual conditions (Fig. 1Ba and b), the box was fixated to a support frame. In the bimanual conditions (Fig. 1Bc and d), the tool was held unsupported between the hands, which implied that the two hands generated forces of virtually the same magnitudes but in opposite directions.

The handles, gripped by the thumb, index and long finger, were equipped with custom-built optometric force transducers that measured compressing and stretching forces along the longitudinal axis of the tool and twist forces around this axis. Application of longitudinal and twist forces moved the cursor horizontally and vertically, respectively. A single hand generated practically identical forces when engaged in the unimanual and in the bimanual conditions because the mean values of the forces at the two handles controlled the cursor in the bimanual conditions. With zero force, the cursor was in the middle of the screen and its position relative to the center of the screen scaled linearly with force. An optoelectronic device measured tool movements used to determine primarily acting hand (Johansson et al., 2006).

The manual actions translated into cursor movements by two different mapping rules. With one of these rules, the cursor moved rightwards when the tool was subjected to longitudinal compression forces and upwards with twist forces applied in the counterclockwise direction (Figs. 1Ba and c). Hence, the cursor moved directionally with the forces applied by the left hand. This rule was applied in one bimanual condition where it rendered the subjects to use the left hand as prime actor (Fig. 1Bc) (Johansson et al., 2006) and when the left hand acted in the unimanual condition (Fig. 1Ba). For the other mapping rule, the cursor moved with the forces applied by the right hand. That is, it moved leftward with longitudinal compression forces and upward with clockwise twist forces. This rule was applied in the other bimanual condition where it rendered the right hand as prime actor (Fig. 1Bd) (Johansson et al., 2006) and in the unimanual condition in which the right hand acted (Fig. 1Bb). A target hit required that the cursor was inside the target zone for ≥ 15 ms, and once hit, the target immediately jumped by a distance of 8.8° visual angle to a new unpredictable position on the screen. The target was presented at 44 different positions on the screen, equally distributed across the four quadrants (Fig. 1A). On average, the targets were located $4.7 \pm 0.7^\circ$ (mean ± 1 SD) from screen center, which corresponded to 2.2 ± 0.3 N tangential force applied to one of the handles in the unimanual conditions or between the handles in the bimanual conditions.

A 1.5T Philips Gyroscan ACS NT scanner (Philips Medical Systems, Eindhoven, The Netherlands) was used to collect one fMRI scan of the whole brain every 3 s. A gradient-echo sequence provided multi-slice T2*-weighted images (echo time = 50 ms, flip angle = 90° and in-plane resolution = 3.44×3.44 mm² in a 64 by 64 matrix). An image volume comprised 33 continuous slices of 4.4-mm thickness (no interslice gap). A microcomputer-based system (SC/Zoom, Physiology Section, IMB, Umeå University, Sweden) digitized and stored transducer signals and managed target presentations, assessed target hits and administrated the fMRI scanning protocol.

Experimental protocol

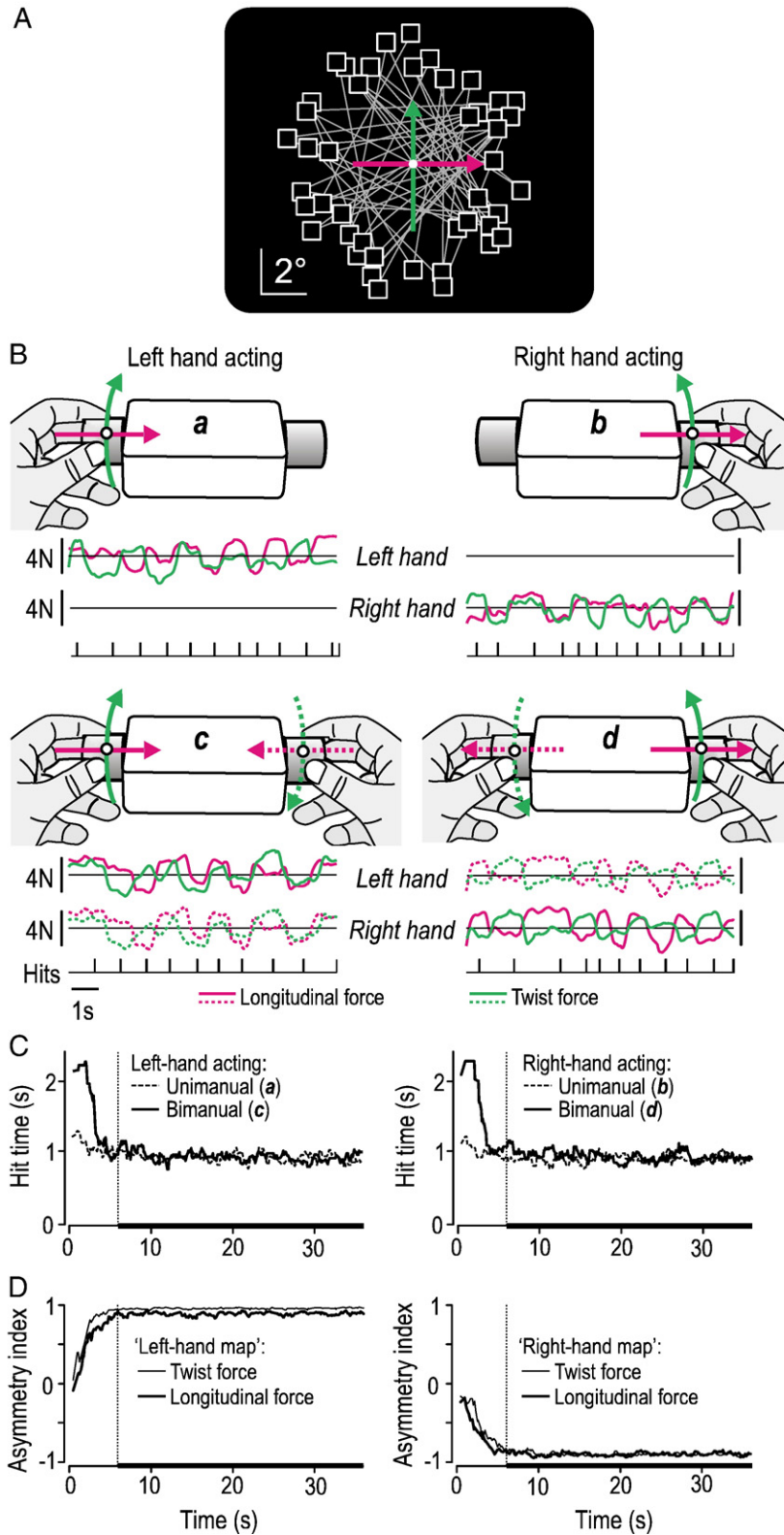
Because the present task was novel, it had to be learnt (Sailer et al., 2005). All subjects trained on the four experimental conditions across 5 days before scanning and had reached a stable performance at the end of training (for details see Johansson et al., 2006). They participated in four consecutive fMRI scanning sessions that each included the four conditions. The order of presentation of the four conditions varied across the scanning sessions in a manner unpredictable to the subject and the overall order of conditions was counterbalanced across subjects. Between scanning sessions, there were 2-min breaks during which the subjects were reminded to hit the targets as fast as possible.

During an 18-s preparation period preceding each action period that lasted 36 s, the screen displayed a drawing that instructed the subjects about how to grip the tool by showing it held by either the right, left or both hands. When the drawing appeared, the subject gripped the tool accordingly and then held it while waiting for a change of the display to show instead the cursor and the first target, which triggered the onset of the action period. The extinction of the cursor and target and appearance of a crosshair in the center of the screen ended the action period. This event cued the subject to release the tool and rest while watching the crosshair. After 18 s, a new preparation period commenced. To cope with T1 equilibration effects, before each scanning session we collected five surplus scans during which the screen displayed the crosshair.

Analysis

We measured subjects' performance by the time between sequential target hits (hit time) and by a cursor path index related to the straightness of the cursor trajectories between successive

targets defined as the ratio between the distance the cursor traveled and the actual inter-target distance. For the bimanual conditions, we calculated one hand asymmetry index for longitudinal forces and one for twist forces by computing the correlation between longitudinal forces and lateral tool movements, and between twist



forces and tool rotations, respectively (Johansson et al., 2006). These movements were small and for a typical cursor transition between successive targets, the lateral movement was some 2 mm and the rotational one around 2°. A significant positive and negative index indicates left- and right-hand as prime actor, respectively (for further details see Johansson et al., 2006).

To represent steady-state adapted behavior in the present results, we analyzed fMRI images obtained during the last 30 s of the 36-s-long action periods. Accordingly, for the same 30-s periods, we calculated median values of behavioral variables obtained for each subject and experimental condition for use in repeated measure ANOVAs. During the first 6 s of the action periods, the hit time (and path index) decreased (Fig. 1C) in all conditions. For the bimanual conditions, subjects identified the mapping rule and the hand asymmetry indices polarized according to the prevailing mapping rule during this period (Fig. 1D). We used repeated measure ANOVAs to justify the selection of the last 30 s to represent steady-state behavior. In these analyses, applied to each performance variable, we divided the 36-s action periods in six 6-s epochs, and for each subject, experimental condition and epoch we computed the median values for each variable. A planned comparison addressing the last five epochs showed no effect of epoch on any performance variable ($0.20 \leq F_{(4,60)} \leq 1.95$; $P \geq 0.11$ in all instances). As expected, except for the path index in the unimanual conditions, epoch had a significant effect on all variables if also the first 6-s epoch was included in the ANOVAs ($6.1 \leq F_{(5,75)} \leq 45.6$; $P \leq 0.0001$ in all instances).

For analysis of fMRI data, we used the Statistical Parametric Mapping software (SPM2; <http://www.fil.ion.ucl.ac.uk/spm/>; The Wellcome Department of Cognitive Neurology, London, UK). The functional images were resliced, realigned, unwarped to correct for head movements, normalized (linear and non-linear transformation) to the format of the Montréal Neurological Institute (MNI) brain template ($2 \times 2 \times 2$ mm³ voxel size), and smoothed with an isotropic Gaussian kernel of 10 mm (FWHM). High-pass filtering (2.3 MHz) reduced subject-specific drifts in signal and proportional grand mean scaling applied over each scanning session reduced slow global changes in activity. For each subject, we fitted a general linear model to the data ('first level analysis'; Friston et al., 1999). Eleven different 'boxcar' regressors modeled the various functional states of the subjects during the scanning. Three regressors represented the preparation periods (left-hand, right-hand, and bimanual grips), and for each experimental condition we defined one regressor for the first 6 s of the action period (i.e., a total of 4 regressors) and one for the remaining 30 s (i.e., a total of 4 regressors). We convolved the regressors with the standard canonical hemodynamic response function and the general linear model provided the relevant contrast images for each of the 16 subjects. Given our focus on the steady-state performance, the

regressors pertaining to the first 6-s period of target chasing represented states of no interest. This also applied to the regressors pertaining to the preparation periods, except in one analysis as detailed in the Results section.

The single-subject images were then entered into a random effects group analysis ('second level analysis'; Friston et al., 1999). For each voxel we conducted a 2×2 factorial ANOVA on the BOLD responses where we used F -tests to assess the main effect of acting hand (left, right) and of grip type (unimanual, bimanual), and regions with interaction effect (cf. Fig. 1B). We adopted a P -value threshold of 0.01 after whole brain correction for multiple comparisons using the false discovery rate (FDR) algorithm (Genovese et al., 2002). We examined BOLD effect sizes at the level of clusters to resolve the nature of significant effects as indicated by the ANOVA. For analyses of specific contrasts within the primary sensorimotor cortices (post hoc comparisons) as itemized in the Results section, the relevant contrast images for each of the 16 subjects were entered into a random effects group analysis where one-sample t -tests were used to label regions of activity changes (P -value threshold of 0.01).

We performed a conjunction analysis (Nichols et al., 2005) to assess brain regions jointly activated in all four experimental conditions. Based on functional images for the action periods of each condition and subject, we obtained the comparisons in the conjunction analysis by means of multiple regression in SPM2. In this analysis we applied the more conservative family wise error (FWE) correction to account for multiple comparisons (P -value threshold=0.01) because in contrast to the factorial analysis that targeted differences in activity between defined action states, this analysis was sensitive to an activity related to action as such on which task-related activity can be considered superimposed. To assess statistically laterality effects (see Results sections), for each subject we measured the average BOLD signal change (beta-values) both for the voxels identified by the conjunction analysis and for the corresponding voxels of the contralateral hemisphere obtained by reversing the x -coordinates. For each cluster, we then ran a one-tailed paired t -test on the BOLD signal change (P -value threshold of 0.01; $df=15$).

The anatomical localization of local maxima (and clusters) based on coordinates provided in MNI stereotaxic space was assessed by the automated anatomical labeling software (Tzourio-Mazoyer et al., 2002) and cross-referenced to the Talairach stereotaxic atlas (Talairach and Tournoux, 1988) after appropriate coordinate transformations (www.mrc-cbu.cam.ac.uk/Imaging/) and for the cerebellum by reference to the Schmammann et al. (1999) atlas. For the frontal cortex, we have used the nomenclature proposed by Picard and Strick (2001). Minimum required spatial cluster extent was 20 voxels and local maxima had to be separated by at least 10 mm. Visualization of significant effects on brain

Fig. 1. Apparatus, grip types and target distribution on screen. (A) Distribution of target positions (squares) where consecutively appearing targets are connected with a straight line. The cursor is shown at scale in the center of the screen (white dot). (B) Tool used by the subjects to control the cursor and the 2×2 factorial design with four experimental conditions: unimanual grip with left (a) and right (b) hand acting and bimanual grip with left (c) and right (d) hand as prime actor. Note that the term 'acting hand' is used for both grip types and for the bimanual grip, it refers to the primarily acting hand. The corresponding solid line arrows in panels A and B indicate the mapping rules relating hand forces and torques to cursor movements. Longitudinal compression forces (magenta) could either move the cursor to the right (a and c) or to the left (b and d) whereas counterclockwise twist forces (green) could move the cursor either upwards (a and c) or downwards (b and d). Superimposed time traces of the lower panels show forces applied by a single subject during 10 s of target chasing in the scanner. Bottom trace represents instances of target hits (spikes). In the bimanual condition, forces generated by the primarily acting hand (solid line curves and arrows) were always counterbalanced by opposing forces generated by the cooperating, assisting hand (dotted line curves and arrows). (C and D) Hit time as a function of time for unimanual and bimanual conditions with left and right hand acting and hand asymmetry index recorded during the bimanual conditions for longitudinal and twist forces. Median values for all subjects based on data computed for a ± 1 s sliding time window (for details see Johansson et al., 2006). Vertical line and embossed segment of the abscissa delimit the period used in fMRI and behavioral analyses.

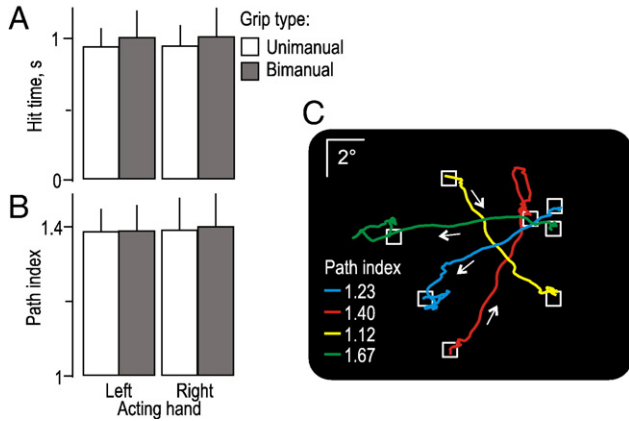


Fig. 2. Subjects' performance in the scanner. Hit time (A) and path index (B) for all four experimental conditions. Height of columns gives mean value across subjects and error bars indicates unilaterally 1 SD ($N=16$). (C) Cursor trajectories between successive targets and corresponding path indices exemplified for 4 target transitions by a single subject. Arrows indicate direction of cursor movement.

templates and plots of effects in histograms were done using in-house developed software (DataZ, Physiology Section, IMB, Umeå University, Sweden).

Results

We present the results in three main sections. First, we address the subjects' behavior in the fMRI scanner. Second, based on the factorial design of the experiment (Fig. 1B), we examine main effects of acting hand (left, right) and grip type (unimanual, bimanual) and interactions between these factors on the BOLD signals. For the bimanual conditions, the term acting hand refers to the hand functioning as prime actor. Finally, based on the conjunction analysis we examine BOLD activity that was common for all four experimental conditions. Note that the present results refer to the steady-state adapted behavior during the action periods (see Materials and methods).

Performance in the fMRI scanner

Target hit time and path index were similar across all experimental conditions (Figs. 2A and B). A repeated measure ANOVA on the path index revealed neither an effect of grip type

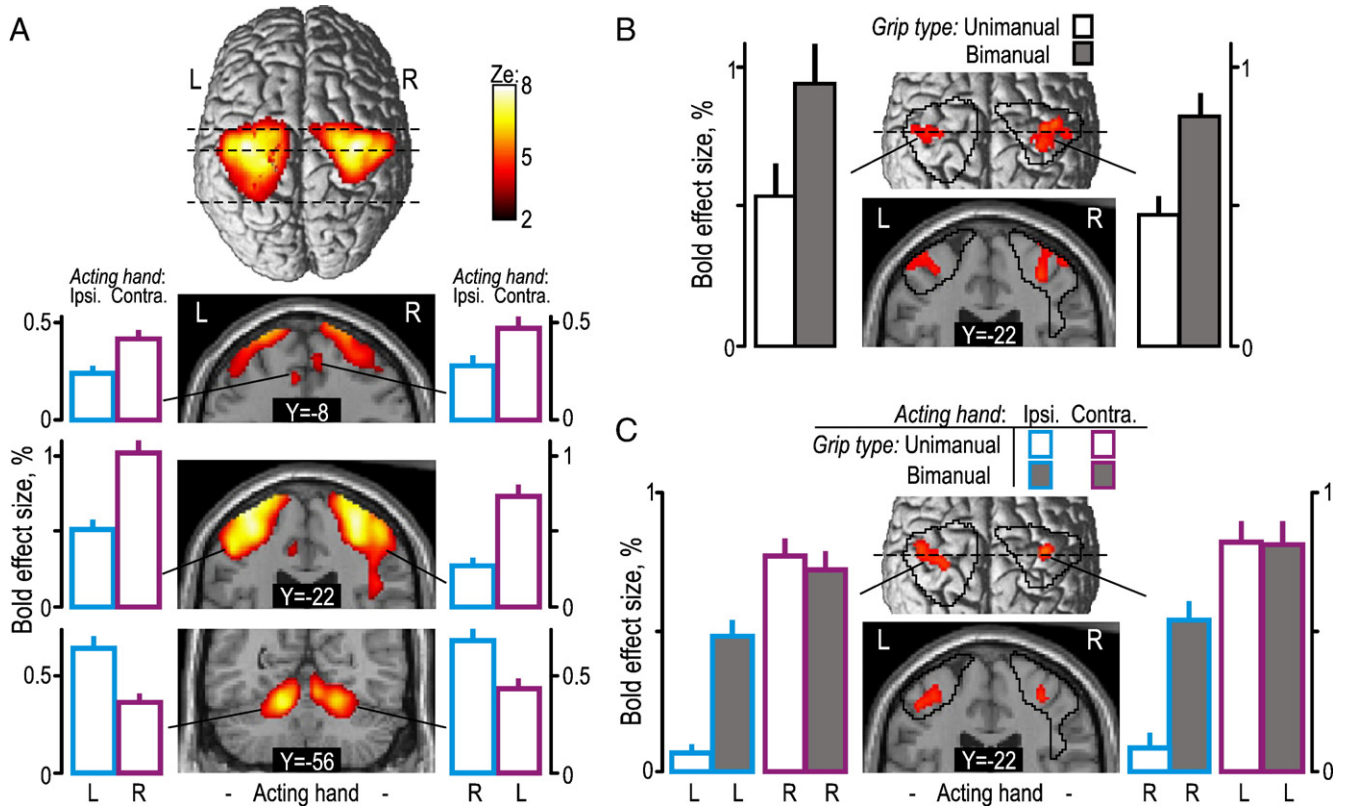


Fig. 3. Factorial analysis of effects of acting hand and grip type on brain activity averaged across subjects. (A, B and C) Areas with main effect of acting hand (Table 1), main effect of grip type (Table 2) and interaction effects of acting hand and grip type (Table 3), respectively. Surface rendered diagrams (render depth=20 mm), based on single-subject standardized brain template in SPM2, refer to the dorsal view of the brain and horizontal dashed lines indicate the location of the coronal slices of the MNI T1-weighted brain template on which labeled areas are superimposed. Thin black lines in panels B and C outline areas with main effect of acting hand (cf. A). BOLD effect sizes are shown to interpret functionally the effects revealed by the ANOVA; labeling of a brain area indicates the presence of a significant effect but not its nature. Histograms give, for each level of the factors examined (coded by the column's outline color and/or fill), the percent BOLD signal change within the identified clusters relative to mean of session. Height of columns gives mean value across subjects and vertical lines represent unilaterally 1 SE ($N=16$). R, right; L, left; Ipsi., ipsilateral; Contra., contralateral; coordinates in MNI stereotaxic space.

Table 1
Main effect of acting hand (left, right)

Number of voxels	Region	X	Y	Z	Peak Ze
<i>Right > Left</i>					
3470	L precentral gyrus (BA 6)	-38	-18	68	7.9
	L precentral gyrus/Central sulcus (BA 4)	-26	-28	78	7.3
	L postcentral gyrus (BA 3)	-46	-20	50	6.7
89	L cingulum gyrus (BA 24)	-6	-8	46	4.1
	L cingulum gyrus/Paracentral lobule (BA 31)	-8	-22	56	3.8
1567	R cerebellum (Lo V; intermediate zone)	16	-48	-24	6.9
		8	-56	-14	5.7
	R cerebellum (Flocculus)	34	-36	-38	3.5
<i>Left > Right</i>					
3389	R precentral gyrus (BA 4)	34	-18	58	7.9
	R precentral sulcus (BA 6)	24	-16	78	6.9
	R postcentral gyrus (BA 3/BA 1)	48	-22	58	6.3
	R postcentral gyrus/Rolandic Operculum (BA 48)	46	-22	24	4.4
65	R medial frontal gyrus/SMA (BA 6)	8	-8	58	3.9
1466	L cerebellum (Lo V/VI; intermediate zone)	-14	-58	-20	7

Number of significant voxels is given for each identified cluster (F -test; $P < 0.01$ FDR corrected, random effects group analysis). Hemisphere (L—left; R—right), brain region, Brodmann area (BA) and cerebellar lobule (Lo) refer to coordinates (X , Y , Z ; provided in MNI stereotaxic space) of peak Z equivalent (Ze) values located within each cluster. By comparing the BOLD effect sizes obtained with either hand acting, we assessed brain areas that showed stronger activation with the right vs. left hand acting and vice versa.

($F_{(1,15)} = 0.40$, $P = 0.54$) nor of acting hand ($F_{(1,15)} = 0.19$, $P = 0.67$) and no significant interaction between grip type and acting hand ($F_{(1,15)} = 0.04$, $P = 0.84$). Measured as hit time, however, the performance was marginally better in the unimanual (0.96 ± 0.13 s per target; mean ± 1 SD) than in the bimanual conditions (1.02 ± 0.17 s) ($F_{(1,15)} = 8.97$, $P < 0.01$). There was no effect of acting hand ($F_{(1,15)} = 0.03$, $P = 0.86$) and no interaction effect ($F_{(1,15)} = 0.00$, $P = 0.99$). As previously reported (Johansson et al., 2006), in the bimanual conditions the subjects' reliably selected acting hand according to the prevailing mapping rule (see also Fig. 1D).

Once the target was hit and it appeared at a new location 8.8° away (see Fig. 1A), subjects applied time varying coordinated longitudinal and twist forces (see time traces in Fig. 1B) that launched a cursor movement diagonally on the screen in the direction of the new target position (Fig. 2C). However, once the cursor was near the target, additional movements were usually required to hit it. This homing-in behavior markedly contributed to the rise in the path index above unity (Fig. 2B) and, on the average, it accounted for about 50% of the target transition time (Sailer et al., 2005). In the unimanual conditions, one hand generated coordinated longitudinal and twist forces, whereas the bimanual conditions, in addition, involved coordination between the two hands where they generated simultaneously coordinated mirror-symmetric longitudinal force components and anti-symmetric twist force components. The corresponding muscle activation patterns were symmetric for longitudinal components and asymmetric for

twist components. Even though the bimanual conditions seemed more complex in terms of control, none of the subjects commented on those being more difficult.

Factorial analysis of brain activity

Acting hand

This factor exerted a main effect on the magnitude of BOLD responses bilaterally in the primary sensorimotor cortex (SMC) and adjacent premotor and parietal areas, and bilaterally in the cerebellar hemispheres (Fig. 3A; Table 1). Two clusters, one in each cerebral hemisphere, showed activity maxima in the SMC and in the dorsal lateral premotor area (PMd). In addition, the cluster in the right hemisphere showed one maximum in a ventral lateral premotor area (PMv). As expected, the BOLD responses in these clusters were stronger when the contralateral hand acted as compared to when the ipsilateral one did (see histograms in Fig. 3A). Two clusters that bilaterally engaged cerebellum showed a stronger BOLD response when the ipsilateral hand acted. For the right cerebellum, the activation primarily engaged lobule V with local maxima in the intermediate zone and in flocculus. The cluster in the left cerebellum engaged lobules V and VI with a maximum in the intermediate zone. Thus, changes of acting hand resulted in a between-hemisphere shift in the level of activation of mainly homologous cortical sensorimotor and cerebellar areas. Acting hand also influenced activities in mesial frontal cortex (Fig. 3A; Table 1). Right hand acting rendered stronger activation in the left caudal cingulate zone (CCZ) whereas left hand acting rendered stronger activation in the right supplementary motor area proper (SMA-proper).

Grip type

For one cluster in each hemisphere, we observed a main effect of grip type (unimanual, bimanual). Acting bimanually rendered stronger activation for both clusters. Furthermore, they both engaged SMC and were thus located within the area exhibiting a main effect of acting hand (Fig. 3B; Table 2). The smaller cluster in the left hemisphere (126 voxels) showed three local maxima while that of the right hemisphere (323 voxels) showed four maxima.

Table 2
Main effect of grip type (bimanual, unimanual)

Number of voxels	Region	X	Y	Z	Peak Ze
<i>Bimanual > Unimanual</i>					
126	L precentral gyrus (BA 4)	-34	-22	58	4.5
	L postcentral gyrus (BA 3/BA 1)	-42	-24	68	4.5
		-50	-20	58	4.3
323	R precentral gyrus (BA 4)	42	-16	68	5.1
	R central sulcus (BA 4)	34	-20	54	5.1
	R central sulcus/Precentral gyrus (BA 4)	32	-30	74	4.8
	R postcentral gyrus (BA 3/BA 1)	50	-24	64	4.3

Number of significant voxels is given for each identified cluster (F -test; $P < 0.01$ FDR corrected, random effects group analysis). Hemisphere (L—left; R—right), brain region and Brodmann area (BA) refer to coordinates (X , Y , Z ; provided in MNI stereotaxic space) of peak Z equivalent (Ze) values located within each cluster. By comparing the BOLD effect sizes obtained during the bimanual and unimanual conditions, we assessed brain areas that showed stronger activation during bimanual vs. unimanual conditions and vice versa.

Table 3
Interaction effects of acting hand and grip type

Number of voxels	Region	X	Y	Z	Peak Ze
255	L postcentral gyrus (BA 3)	-46	-18	50	4.9
	L central sulcus (BA 4)	-34	-24	54	4.8
	L precentral gyrus (BA 4)	-38	-18	68	4.3
94	R central sulcus (BA 4)	36	-18	56	5.3

Number of significant voxels is given for each identified cluster (*F*-test; $P < 0.01$ FDR corrected, random effects group analysis). Hemisphere (L—left; R—right), brain region and Brodmann area (BA) refer to coordinates (*X*, *Y*, *Z*; provided in MNI stereotaxic space) of peak *Z* equivalent (*Ze*) values located within each cluster.

The lateralized nature of brain activation in movement implementation might explain this main effect. That is, the SMC contralateral to the acting hand would be activated to a corresponding degree in bimanual and unimanual conditions while the bimanual conditions, in addition, would activate the SMC contralateral to the assisting

hand. This explanation predicts a significant interaction of acting hand and grip type on the BOLD responses for the entire area of main effect of grip type. However, an analysis of interactions revealed a more complex picture, suggesting that bimanual and unimanual activities preferentially engaged subregions of the SMCs.

Interaction effects of acting hand and grip type

Significant interaction was observed in two cortical clusters (Fig. 3C; Table 3), one in the left SMC (255 voxels; 3 local maxima) and a smaller one in the right SMC (94 voxels). Both were buried in the central sulcus, within the regions of main effect of acting hand. However, the cluster in the left hemisphere only partially overlapped with that showing main effect of grip type and the cluster of the right hemisphere represented a subregion of that with main effect of grip type (cf. Figs. 3B and C). The lack of complete match between regions with main effect of grip type and interaction effect suggests functional specialization within the SMC. To explore this possibility further, we analyzed BOLD responses in

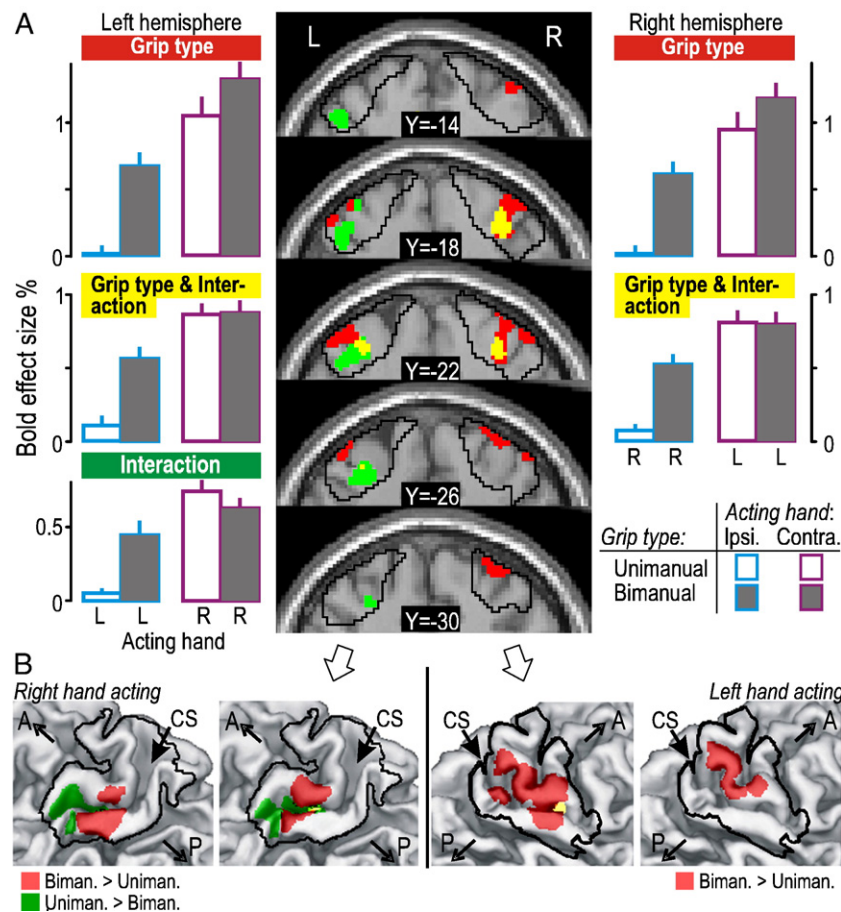


Fig. 4. Areas with bimanual and unimanual preferences within SMC. (A) Coronal slices of the MNI T1-weighted brain template show main effect of grip type masked exclusively with the zone of interaction between grip type and active hand (red), interaction effect masked inclusively with the main effect of grip type (yellow) and interaction effect masked exclusively with the main effect of grip type (green). Histograms give percent BOLD signal change within the delineated zones relative to mean of session. For further details, see caption of Fig. 3. (B) Surface rendered diagrams based on Human Colin atlas surfaces (Fiducial.SPM2) using the freely available Caret software (Van Essen et al., 2001; <http://brainmap.wustl.edu/caret>). Part of left and right hemisphere viewed from a dorso-posterolateral angle. Arrow indicates the medial origin of the central sulcus (CS). Middle diagrams show, for each hemisphere, the same data as shown in coronal slices of panel A using the same color code. The lateral diagrams delineate, for each hemisphere, areas with significant increases in activation when contrasting bimanual versus unimanual actions (red) and unimanual versus bimanual actions (green). A, anterior; P, posterior. (A and B) Black lines outline the clusters defined by main effect of acting hand (see Fig. 3A).

five discrete zones delineated based on differences in statistical outcomes (Fig. 4A): two zones exclusively showed main effect of grip type, one located in each hemisphere (labeled red in Fig. 4A). These zones involved primarily the convexities of the pre- and postcentral gyri. Two other zones, again one in each hemisphere, showed both main effect of grip type and interaction effect (yellow). They appeared located primarily in the anterior bank of the central sulcus. Finally, one zone showed interaction but no main effect of grip type (green). This zone, present only in the left hemisphere according to our extent threshold criterion (20 voxels), was located deep in the central sulcus and involved both pre- and postcentral areas. Two small clusters with 6 and 7 voxels, respectively, located in the depth of the central sulcus of the right hemisphere showed the corresponding BOLD responses (not shown).

In accord with their location in the area of main effect of acting hand, all zones showed stronger BOLD responses when the contralateral hand acted than when the ipsilateral did (cf. columns outlined with blue versus purple in the histograms of Fig. 4A). With the ipsilateral hand acting, they all showed substantially stronger BOLD responses in the bimanual than in the matching unimanual condition (cf. pairs of blue columns). With the contralateral hand acting, however, the pattern of BOLD responses differed between zones (cf. pairs of purple columns). First, for both hemispheres, the zone with a main effect of grip type and no significant interaction effect (red in Fig. 4A) showed a stronger BOLD response in the bimanual as compared to the unimanual condition (cf. purple columns in top histograms of Fig. 4A). This suggests that the neural activity of this zone, which was larger in the right (243 voxels) than in the left hemisphere (98 voxels), showed a preference for bimanual over unimanual actions. A post hoc comparison contrasting bimanual versus unimanual actions (one-sample *t*-test) verified stronger activation of the right SMC when the left hand acted and indicated activity maxima located on the crest of the precentral gyrus ($X, Y, Z = 30, -22, 76; 42, -18, 66$) (Fig. 4B). The corresponding contrast for right hand acting verified stronger activation in the left SMC that involved both pre- and postcentral gyrus with two maxima located on the crest of the postcentral gyrus ($-48, -28, 64; -36, -36, 72$) (Fig. 4B).

The sizeable zone (215 voxels) in the left SMC with an interaction effect but no main effect of grip type (green in Fig. 4) showed stronger BOLD responses when the contralateral (right) hand acted in the unimanual as compared to the bimanual condition (cf. purple columns in the bottom left histogram of Fig. 4A). Contrasting unimanual versus bimanual actions for conditions when the right hand acted verified stronger activation in the depth of the central sulcus and indicated two activity maxima, one located in the precentral and one in the postcentral cortex ($-44, -10, 50; -48, -26, 46$) (Fig. 4B). These results suggest that neural activity in this zone showed a preference for especially unimanual actions performed with the right hand. Finally, for the bilateral zone with both an interaction effect and a main effect of grip type (yellow in Fig. 4), comparable BOLD responses when the contralateral hand acted in the unimanual and the bimanual conditions explained the interaction effect. Hence, this zone showed no preference for bimanual or unimanual actions. The zone in the central sulcus of the right hemisphere was larger (80 voxels) than the corresponding one in the left hemisphere (20 voxels).

Brain areas activated irrespective of grip type and acting hand

Dorsal premotor and posterior parietal areas were activated under all task conditions and most extensively within the left

hemisphere (Fig. 5; Table 4). Regarding premotor activity, one large cluster extended from the mesial frontal cortex, laterally along the left precentral gyrus and the caudal part of the superior frontal gyrus down to the left middle frontal gyrus (#1 in Fig. 5). For the mesial frontal cortex, this cluster extended from about 10 mm anterior to 12 mm posterior to the vertical line through the anterior commissure, suggesting engagement of both SMA-proper and pre-SMA (Picard and Strick, 2001). This mesial activation, however, was separate from the mesial activation defined by the main effect of acting hand (cf. Fig. 3A and Table 1). That is, for the left hemisphere, it was more dorsally located and for the right it had a more anteromedial location. Right premotor activation was limited to two rather small clusters located caudally in the middle frontal gyrus (#4 and #5 in Fig. 5). However, when the left hand

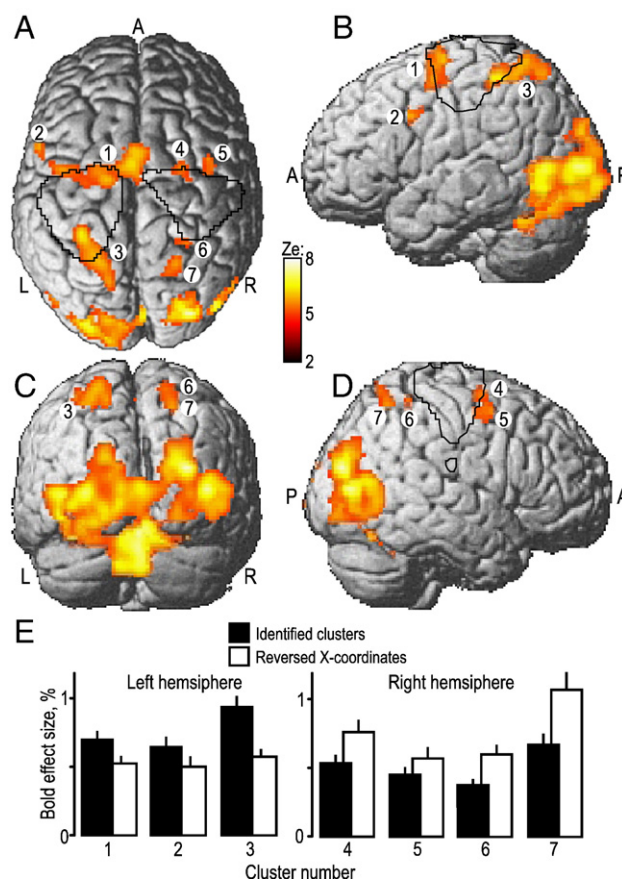


Fig. 5. Fronto-parietal cortical areas engaged irrespective of task condition. (A–D) Common activation across task conditions averaged across subjects (Table 4) rendered on a single-subject standardized brain template in SPM2 viewed from a dorsal (A), left (B), posterior (C), and right (D) aspect (render depth=20 mm; L, left; R, right; A, anterior; P, posterior). Thin black lines correspond to areas activated by main effect of acting hand (see Fig. 3A). Numbers indicate frontal and parietal cortical clusters detected in the left (1–3) and right (4–7) hemisphere. (E) BOLD signal change relative to mean of session for clusters identified in the left and right hemisphere by the conjunction analysis (black columns) and for the corresponding voxels of the contralateral hemisphere (white columns). Height of columns indicates mean values across subjects and error bars give unilaterally 1 SE ($N = 16$). Irrespective of the hemispheric location of a cluster, for all but one (#5) the delineated area in the left hemisphere showed significantly stronger BOLD responses.

Table 4
Areas activated irrespective of grip type and acting hand

Number of voxels	Region	X	Y	Z	Peak Ze
<i>Frontal cortex</i>					
858	L medial frontal gyrus/SMA (BA 6)	-2	-2	56	6.5
	L superior frontal gyrus (BA 6)	-18	-10	68	6.2
	L precentral gyrus (BA 6)	-44	-4	56	5.9
		-30	-12	54	5.3
36	L inferior frontal gyrus (BA 44)	-56	8	36	6.1
59	R middle frontal gyrus (BA 6)	40	2	54	5.7
69	R middle frontal gyrus (BA 6)	26	-4	64	5.7
		26	-8	50	5.3
<i>Parietal cortex</i>					
561	L postcentral sulcus (BA 2)	-32	-40	58	6.8
	L superior parietal lobule (BA 7)	-22	-56	66	6.2
		-16	-68	60	5.9
117	R superior parietal lobule (BA 7)	22	-58	56	5.9
		18	-62	66	5.5
22	R superior parietal lobule (BA 7/BA 5)	28	-46	60	5.6
<i>Occipital cortex</i>					
10516	L calcarine sulcus (BA 17)	-10	-88	0	6.7
		-18	-100	-4	6.7
	L cuneus (BA 18)	-14	-98	16	5.9
	L superior occipital gyrus (BA 19)	-18	-82	14	5.5
		-18	-90	26	6.3
	L inferior occipital gyrus (BA 18)	-24	-88	-10	6.4
	L middle occipital gyrus (BA 18)	-28	-88	6	7.6
	L fusiform gyrus (BA 19)	-28	-74	-12	6.7
		-24	-62	-12	7.5
	L fusiform gyrus (BA 37)	-38	-60	-16	6.7
	R cuneus (BA 18)	4	-88	8	6.8
	R calcarine sulcus (BA 17)	14	-76	8	6.3
	R lingual gyrus (BA 19)	22	-62	-4	6
	R fusiform/Lingual gyrus (BA 18)	24	-86	-4	5.9
	R lingual gyrus (BA 18)	12	-90	-12	5.6
	R superior/Middle occipital gyrus (BA 19)	30	-84	20	>8.1
	R middle occipital gyrus (BA 19)	32	-84	6	5.8
		42	-80	8	7.8
<i>Occipitotemporal junction</i>					
	L inferior/Middle occipital gyrus (BA 19/37)	-42	-70	4	7.3
	L inferior temporal gyrus (BA 19/37)	-42	-68	-6	7
	R middle temporal gyrus (BA 19/37)	44	-68	12	6.7
		48	-64	0	6.2
<i>Cerebellum</i>					
	L cerebellum (Lo V; Vermis)	-4	-60	-2	5.8
	L cerebellum (Lo V; intermediate zone)	-12	-64	-12	7.8
	L cerebellum (Lo VI; intermediate zone)	-8	-70	-36	7
	L cerebellum (Lo VI; lateral zone)	-36	-54	-24	6.6
	R cerebellum (Lo VI; Vermis)	2	-72	-18	7.8
	R cerebellum (Lo VI; intermediate zone)	6	-70	-32	7.5
	R cerebellum (Lo VI; lateral zone)	30	-54	-26	5.3

Table 4 (continued)

Number of voxels	Region	X	Y	Z	Peak Ze
<i>Subcortical</i>					
509	L thalamus	-14	-18	12	6.6
309	R thalamus	14	-16	10	7.1
	R putamen	20	-8	8	5.8

Number of significant voxels is given for each identified cluster ($P < 0.01$ FWE corrected, random effects group analysis). Hemisphere (L—left; R—right), brain region, Brodmann area (BA) and cerebellar lobule (Lo) refer to coordinates (X, Y, Z ; provided in MNI stereotaxic space) of peak Z equivalent (Ze) values located within each cluster.

acted, premotor activity arose in the right hemisphere at locations corresponding to those found in the left hemisphere in all task conditions (cf. outlines of main effect of acting hand and common activations in Fig. 5; see also Johansson et al., 2006). Regarding the parietal lobe, one cluster extended from dorsal precuneus into the postcentral gyrus of the left hemisphere (#3 in Fig. 5). It showed two local maxima dorsally in the superior parietal lobule and one in the postcentral/intraparietal sulcus. Two smaller clusters were located in the right superior parietal lobule (#6 and #7) at locations corresponding to activity peaks observed in the left hemisphere.

These results suggest that the control of the present task, irrespective of acting hand and grip type, engaged a bilateral fronto-parietal network, which activity was biased to the left hemisphere. The latter impression was confirmed by statistically comparing the size of the BOLD response for each of the seven clusters identified in the frontal and parietal lobes with the BOLD response of the corresponding volumes in the opposite hemisphere (Fig. 5E). Although numerous previous reports have indicated a critical role for the left hemisphere in instantiating sensorimotor engrams that support control of skilled movements irrespective of hand assignments (Wyke, 1971; Kimura and Archibald, 1974; Haaland et al., 1987; Kawashima et al., 1993; Kim et al., 1993; Haaland and Harrington, 1996; Weiss et al., 2001; Schluter et al., 2001), it is not yet clear which specific task characteristics that promote left-lateralized activity.

A large bilateral cluster (10 516 voxels) involved parts of cerebellum and occipital cortex (Fig. 5C; Table 4). The cerebellar activation extended bilaterally from the vermis across the intermediate zones into the lateral zones with activity maxima located both in the hemispheres and in the vermis. Eighteen local maxima were observed in the occipital lobe and two in the left and two in the right occipitotemporal junction. The use of vision for the guidance of the hand actions seemed to determine the activation of the occipitotemporal junctions, whereas the main occipital activation reflected a more general use of vision during the present task: a conjunction of images obtained during the action period contrasted against those of the corresponding preparation periods where the subjects watched a drawing of the grasped tool (see Materials and methods) rendered little activation of the occipital lobe but saved that observed for the rest of the brain, including that of the occipitotemporal junctions (Fig. 6A). Moreover, a conjunction of images obtained during the preparation periods determined bilateral activation only in the occipital lobe (Fig. 6B). The location of the bilateral activation in the occipitotemporal junctions corresponded to that of a previously described extrastriate visual area (MT/hMT/V5+) implicated in perception of moving stimuli (Watson et al.,

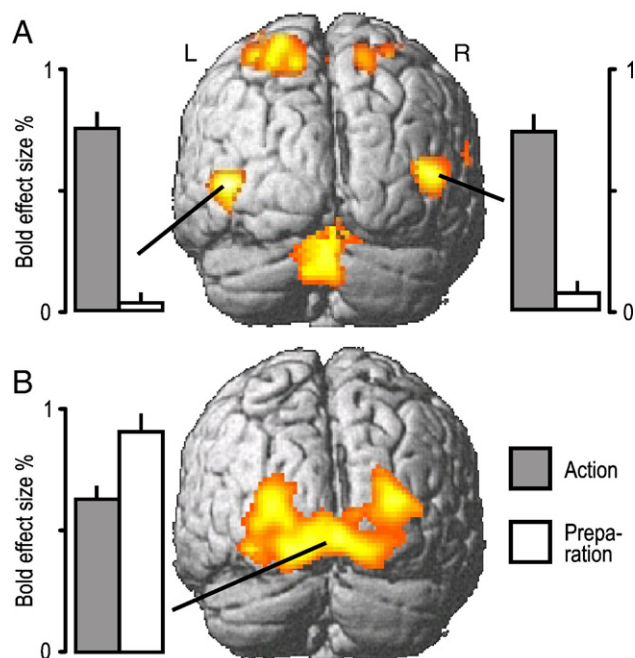


Fig. 6. Action as compared to action preparation activated occipitotemporal junctions. (A) Conjunction of images obtained during the action periods of all task conditions contrasted against those obtained during the corresponding preparation periods rendered on the posterior aspect of the single-subject standardized brain template in SPM2. Notably, activations pertaining to the occipital and temporal lobes were limited to the occipitotemporal junctions with peak values (X, Y, Z) at $-44, -70, 4$ and $48, -66, 10$ ($Z_e > 7$ in either case). (B) Conjunction of images obtained during the preparation periods of all task conditions with reference to rest showing bilateral activation in the occipital lobe but not in the occipitotemporal junctions. (A and B) Conjunction analysis conducted as described in Materials and methods referring to the main conjunction shown in Table 4 ($P < 0.01$, FWE-corrected). Histograms show average BOLD signal changes within the identified clusters, normalized to mean of session. Height of columns give means across subjects and vertical lines represent unilaterally 1 SE ($N = 16$). L, left; R, right.

1993; Tootell et al., 1995). The increased activation of this area during the action periods corroborates the view that it also supports control of visuomotor tasks (Grefkes et al., 2004; Schenk et al., 2005) and represents a major route for visual input to the dorsal stream pathway (Goodale and Milner, 1992; Goodale et al., 2004). The activations depicted in Fig. 5 thus outlines the most essential cortical elements of this pathway as expressed in the present object manipulation task.

For subcortical areas, we observed bilateral activation in lateral thalamic nuclei (Table 4). For the left hemisphere, it extended into the superior colliculus and for the right into the adjacent striatum with a distinct local maximum in the medial globus pallidus.

Discussion

We have examined brain activity in healthy right-handers while they through tool manipulation accomplished the same task under unimanual and bimanual conditions. A single hand performed virtually identical actions whether the task was unimanually or bimanually performed. Furthermore, in contrast to previous studies comparing neural control mechanisms in bimanual and unimanual actions, the acting hand was factored into the present analysis not

only for unimanual but also for bimanual actions. Likewise, rather than the two hands managing separate goals – as in traditional bimanual experiments – the hands worked towards a common goal as in ordinary manipulations. Our results contradict the widespread notion that complex bimanual coordination requires stronger engagement of non-primary cortical areas and subcortical structures than when the corresponding movement components are performed unimanually (see Introduction). Furthermore, our results suggest that the engagement of medial wall premotor areas in object manipulation rather depends on the primarily acting hand than on whether the task is performed unimanually or bimanually. In seeking for the ‘bimanual coordination controller,’ we found reliable effects of grip type only in the SMC, where we observed zones with preference for bimanual and unimanual activity. We discuss each of these findings further below.

Common engagement of brain areas in bimanual and unimanual action

In contrast to the unimanual conditions, the bimanual conditions required complex interlimb coordination that involved combinations of symmetric and asymmetric muscle activation patterns. Yet, bimanual performance was neither associated with signs of intermanual interferences, as emphasized in previous studies of bimanual coordination (for a review see Swinnen, 2002), nor with stronger activation of brain structures previously associated with increased coordinative complexity (e.g., Debaere et al., 2004; Wenderoth et al., 2005). That the two hands cooperated towards common spatial goals as in most natural situations rather than aiming simultaneously for separate goals as in most studies of bimanual coordination (Swinnen, 2002) presumably explains these differences. Recent evidence suggests also that performances of bimanual gestures might improve with unified goal representations (Lee et al., 1995; Byblow et al., 1999; Mechsner et al., 2001). There is indeed evidence that simultaneous processing of separate action goals not only may compete for partly the same neural resources but it may also engage brain regions not activated by the component tasks when performed in isolation (Roland and Zilles, 1998; Herath et al., 2001; Schubert and Szameitat, 2003). That the brain flexibly appoints one or the other hand as prime actor in bimanual object manipulations presumably reflects a control strategy that prevents interference effects akin to those occurring during simultaneous execution of different sensorimotor transformations (Johansson et al., 2006).

Although our subjects used the fingertips for precise object manipulation, we observed activation of dorsal parietal and premotor cortical areas previously implicated in the control of reaching for visible objects in both macaques (Shen and Alexander, 1997; Wise et al., 1997; Andersen and Buneo, 2002; Picard and Strick, 2003) and in humans (Goodale and Milner, 1992; Kawashima et al., 1995; Grafton et al., 1996; Connolly et al., 2000; Simon et al., 2002; Astafiev et al., 2003; Grefkes et al., 2004; Prado et al., 2005). Notably, we observed little activity in the inferior parietal lobule and in ventral premotor areas, previously implicated in grasping and object manipulation in macaques (Rizzolatti et al., 1988, 2002; Sakata et al., 1997; Graziano and Gross, 1998; Maravita and Iriki, 2004) and humans (Binkofski et al., 1998, 1999; Ehrsson et al., 2000, 2001, 2003; Inoue et al., 2001; Kuitz-Buschbeck et al., 2001; Culham et al., 2003; Stoekel et al., 2003; Johnson-Frey et al., 2005; Schmitz et al., 2005). We interpret this to suggest that the functional distinction between the

dorsal and the ventral parts of the fronto-parietal circuitry relates to the conceptualization of tasks rather than to their effectuation in terms of distal and proximal movement organization as previously thought (see for Refs. Dum and Strick, 2005). We propose that the dorsal part supports actions with goals specified in external visuospatial reference frames irrespective of the mode of effectuation. For the ventral part, we propose that it primarily controls object-oriented actions with goals specified in body or object centered frames of reference, such as when we grasp objects or use tools for gathering purposes or when haptically exploring objects.

Implementation of hand selection

Mesial frontal cortex has been implicated in various aspects of control of single limb tasks (Deiber et al., 1991, 1999; Deecke and Lang, 1996; Passingham, 1996; Hoshi and Tanji, 2004), including visually guided reaching (Picard and Strick, 2003; Crutcher et al., 2004). Furthermore, it has since long been implicated in bimanual coordination (Brinkman, 1984; Wiesendanger and Serrien, 2004), a contention supported by numerous human brain imaging studies (e.g., Sadato et al., 1997; Goerres et al., 1998; Stephan et al., 1999a,b; Toyokura et al., 1999; Immisch et al., 2001; Meyer-Lindenberg et al., 2002; Ullén et al., 2003; Debaere et al., 2004). However, the medial wall activity in the present study did not depend on if the subjects performed the task bimanually or unimanually. One factor that may have contributed to this discrepancy with previous studies is that these did not keep track of prime actor in bimanual conditions. That is, rather than grip type we found that acting hand influenced the activity of medial wall areas. Similar tendencies have previously been reported for unimanual actions (Sadato et al., 1997; Stephan et al., 1999b; Kuhtz-Buschbeck et al., 2003).

Control of interhemispheric communication must be critical for skilled actions that are governed by an asymmetric brain, such as object manipulations that depend on left-lateralized sensorimotor processes (see Results section). The dense connections between homologous mesial frontal areas (Rouiller et al., 1994; Liu et al., 2002; Marconi et al., 2003) and their close interconnections with lateral premotor areas (Dum and Strick, 2005) suggest a prime role of medial wall areas in control of hand selection in unimanual as well as in bimanual conditions. Speculatively, the stronger activation of the left CCZ with right hand acting might reflect a role of this zone in preventing inappropriate action tendencies of the left hand, while simultaneously facilitating right hand actions. Conversely, the stronger activation of the right SMA-proper with left hand acting might reflect a mechanism whereby the brain funnels information from the left to the right hemisphere for implementing left hand lead. In this vein, we have recently proposed that appointment of the left hand as prime actor is realized by the left premotor areas suspending the lead of the left SMC while transposing it to the right SMC by engaging premotor networks of the right hemisphere (Johansson et al., 2006). In addition to transcallosal connections, bilateral information exchange is possible via commissural fiber systems at various levels of the neural axis. For example, bilaterally projecting corticospinal pathways that originate in especially mesial wall areas are likely to contribute to the preparation and modulation of the excitability of intrinsic spinal sensorimotor circuitry (Maier et al., 2002) and might support the control of the assisting, or “postural”, hand in bimanual object manipulation (Viallet et al., 1992).

Bimanual and unimanual preferences within the primary sensorimotor cortex

We identified regions in the SMC contralateral to the acting hand that showed preference for either bimanual or unimanual activity. These results suggest the existence of partly spatially segregated subpopulations of neurons preferentially activated in the bimanual and unimanual conditions, respectively. Indeed, recent studies in monkeys indicate that the primary motor cortex contains subpopulations of neurons tuned for contralateral, ipsilateral and bilateral arm movements (Donchin et al., 1998, 2002; Kermadi et al., 1998, 2000; Kazennikov et al., 1999; Steinberg et al., 2002). These studies also indicate similar types of neurons in dorsal and medial premotor areas and in posterior parietal cortex. Assuming a similar arrangement in humans, the appearance of preferential zones only in the SMC may result from a higher degree of spatial segregation of tuned neurons in this area than in the other areas.

The zone with bimanual preference was more extensive in the right than in the left hemisphere in our right-handed subjects. This may reflect a proportionally more frequent engagement in natural bimanual activities of the left as compared to the right hand. Similarly, that the zone of unimanual preference was markedly left lateralized may reflect a proportionally more frequent engagement of the right hand in unimanual activities related to its superior skills for certain tasks. This zone was located in the depth of the central sulcus, which surface in right-handers is considered greater in the left than in the right hemisphere (Amunts et al., 1996, 2000; Foundas et al., 1998; Mangin et al., 2004).

For the precentral gyrus, the identified zones appear to correspond to two primary motor representations of the hand, one located in the convexity of the gyrus and the other in the depth of the central sulcus (Strick and Preston, 1982a,b; Picard and Smith, 1992; Geyer et al., 1996; Naito et al., 1999). Because these precentral areas also comprise somatosensory representations pertaining to afferent information from deep and cutaneous mechanoreceptors, respectively, these motor representations are thought to support primarily proprioceptive and tactile guidance of manual actions. Hence, the crestal location of the zone with bimanual preference suggests that the bimanual conditions relied more on proprioceptive inputs than the corresponding unimanual ones. Conversely, the sulcal location of the zones that did not show bimanual preference agrees with a critical role of tactile afferent signals in the control of the hand while interacting with environmental objects, whether or not it acts unimanually or together with the other hand. Interestingly, recent evidence in monkey indicates that only the sulcal representation makes monosynaptic connections with motoneurons of finger muscles (Rathelot and Strick, 2006). The location of the postcentral parts of the zones with unimanual and bimanual preference suggests that they represented sensory information that modality-wise complemented that of the precentral somatosensory representations. That is, while the precentral part of the zone with bimanual preference would represent proprioceptive states, the postcentral part would primarily represent tactile states by involving area 1 in the convexity of the gyrus (and perhaps area 3b) (Kaas, 1983; Burton et al., 1997; Iwamura, 1998; Moore et al., 2000). Conversely, the postcentral part of the zone with unimanual preference, which presumably involved area 3a located in the depth of the central sulcus, would have represented proprioceptive rather than tactile states.

In conclusion, we challenge the widely held notion that the control of complex bimanual actions more heavily engages non-primary sensorimotor areas, including medial wall premotor areas, than the control of the corresponding unimanual action components. We submit that the control of bimanual and unimanual object manipulations partly depends on neural processing in different subregions of the primary sensorimotor cortex and that the manifestation of these subregions shows hemispheric asymmetry.

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