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Goal-Selection and Movement-Related Conflict during Bimanual Reaching Movements

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Conflict during bimanual movements can arise during the selection of movement goals or during movement planning and execution. We demonstrate a behavioral and neural dissociation of these 2 types of conflict. During functional magnetic resonance imaging scanning, participants performed bimanual reaching movements with symmetric (congruent) or orthogonal (incongruent) trajectories. The required movements were indicated either spatially, by illuminating the targets, or symbolically, using centrally presented letters. The processing of symbolic cues led to increased activation in a left hemisphere network including the intraparietal sulcus, premotor cortex, and inferior frontal gyrus. Reaction time cost for incongruent movements was substantially larger for symbolic than for spatial cues, indicating that the cost was primarily associated with the selection and assignment of movement goals, demands that are minimized when goals are directly specified by spatial cues. This goal-selection conflict increased activity in the pre–supplementary motor area and cingulate motor areas. Both cueing conditions led to larger activation for incongruent movements in the convexity of the superior parietal cortex, bilaterally, making this region a likely neural site for conflict that arises during the planning and execution of bimanual movements. These results suggest distinct neural loci for 2 forms of constraint on our ability to perform bimanual reaching movements.

Keywords: bimanual, fMRI, human, parietal lobe, reaching

Introduction

Many skilled behaviors involve the coordination of both hands (Guiard 1987). For example, opening a jar requires that 1 hand grasp the jar while the other twists the lid. This action demands tightly integrated control of the 2 hands. In other behaviors, efficient performance requires that the 2 hands perform with relative independence such as when we pick through cherries at the marketplace.

Limitations in producing bimanual movements can illuminate the underlying functional architecture of the action system (Kelso 1984; Franz and others 1996; Heuer and others 2001; Swinnen 2002). Compared with symmetric movements, people are slower to initiate asymmetric movements and exhibit spatial assimilation effects between the 2 trajectories (Heuer and others 2001). The source of these constraints has been extensively debated in the motor control literature. One hypothesis states that processes involved in movement planning and execution are facilitated for spatially symmetric movements through interhemispheric communication (Franz and others 1996; Kennerley and others 2002) or ipsilateral corticospinal pathways (Carson 2005). An underlying assumption here is that the tendency to mirror symmetric movements has evolutionary roots in phylogenetic older behaviors, such as locomotion, and that additional neural processes are needed to modify synergistic tendencies for asymmetric movements. We describe this kind of interference as movement-related conflict.

However, the preference for symmetric movements is dependent on the manner in which the actions are cued (Mechsner and others 2001; Swinnen 2002). Diedrichsen and others (2001) had participants perform bimanual reaching movements, with each hand reaching forward or sideways (Fig. 1*A*). The resulting trajectories could be congruent, in mirror-symmetric directions, or incongruent, in orthogonal directions. Movements were cued either symbolically (a letter indicated the target for each hand) or spatially (the stimuli appeared directly at the target locations). Reaction times (RTs) were considerably slower for incongruent than for congruent movements but only for symbolic cues; with spatial cues, minimal difference in RT was observed. Given that movement planning and execution are similar for both cueing conditions, this dissociation suggests that the RT cost associated with asymmetric movements is mainly due to the conflict related to the translation of the symbolic cues into their associated responses. When 2 different symbolic cues are presented, this translation process is required for each cue and the responses must be assigned to the correct hand. We refer to interference arising at this level as goal-selection conflict. With spatial cues, the movement goals are directly and externally specified, eliminating or minimizing the translation and assignment operations.

We used functional magnetic resonance imaging (MRI) to identify neural regions related to goal-selection and movement-related conflict. Movement-related conflict reflects interactions of movement parameters during planning or execution (Heuer and others 2001). This form of conflict would therefore be associated with higher activation for incongruent than for congruent movements for both symbolic and spatial cues. In particular, we predicted that this form of activity would be observed in the supplementary motor area (SMA), implicated by numerous studies in the production of nonsymmetric bimanual movements (Brinkman 1984; Sadato and others 1997; Jäncke and others 2000; Debaere and others 2001; Steyvers and others 2003).

In contrast, areas required to resolve goal-selection conflict should be more active during incongruent movements compared with congruent movements but only with symbolic cues. This form of conflict may arise in areas associated with the mapping of arbitrary stimuli onto their associated responses. Previous evidence suggests involvement of left parietal (Rushworth and others 2003) and premotor cortex (Grafton and others 1998; Eliassen and others 2003) in this translation process. We will be able to characterize this network for our task by

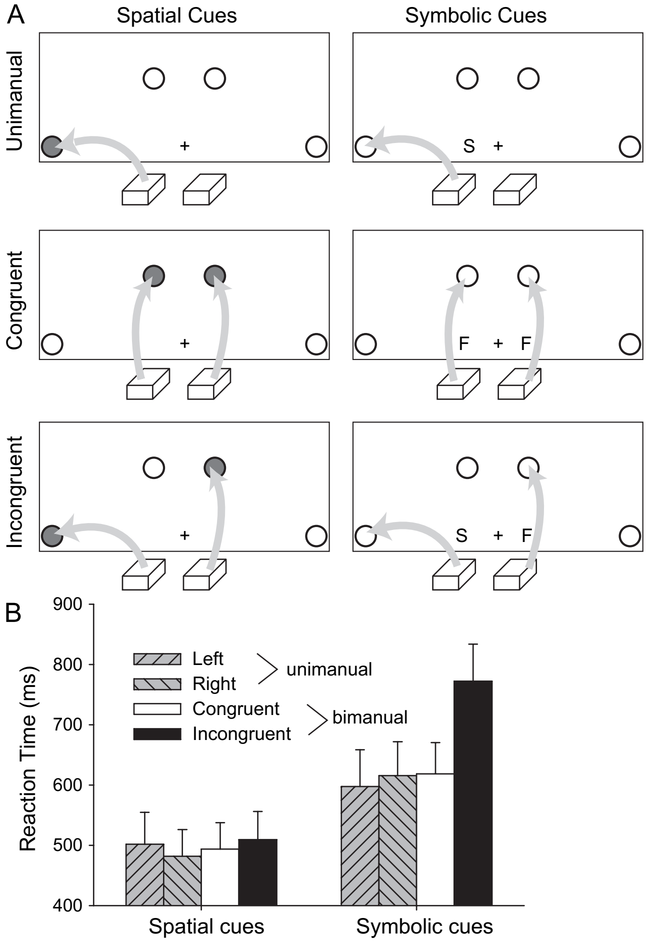

Figure 1. Experimental tasks and behavioral results. (*A*) Movements (light gray arcs) began at the starting locations (boxes) and were executed to target circles, either forward or sideways. The movements were cued by illuminating the target circle (spatial cues) or by letters indicating the movement direction (symbolic cues). Testing included unimanual (left hand or right hand), bimanual congruent (movements were both forward or both sideways), and bimanual incongruent movements (movements were orthogonal). (*B*) RTs showed a strong cost for incongruent movements when symbolically cued. A small but reliable congruency effect was also found for the spatial cues.

comparing unimanual and bimanual congruent movements in the symbolic cueing condition with those in the spatial cueing condition. We can then ask whether areas that show goal-selection conflict lie within this network. Alternatively, goal-selection conflict may engage additional regions, not involved in the translation process itself, such as pre-SMA or the anterior cingulate, which are associated with response conflict in a wide range of tasks (MacDonald and others 2000; Garavan and others 2003; Nachev and others 2005).

Materials and Methods

Participants

Nineteen right-handed participants (Oldfield 1971) (age 18–31 years, 6 men and 13 women) were recruited through advertisements. The data from 4 participants were excluded from the analysis: 2 because of strong head movement-related artifacts and 2 because they, despite instructions, initiated the bimanual movements sequentially rather than simultaneously. Experimental and informed consent procedures were approved by the Institutional Review Board of Dartmouth College.

Procedure

Participants lay supine on the MRI gurney with both hands resting on a nonferrous response board. To minimize head movements, we restricted “reaching” to movements about the wrist and index finger with the elbow and proximal arm firmly supported. For each hand, the required movement could be either “forward” or “sideways.” A forward movement primarily required extension of the wrist and, to a lesser extent, extension of the index finger. A sideways movement primarily required rotation of the forearm and wrist, as well as extension of the wrist and index finger.

The stimuli were presented on a rear projection screen, positioned directly in front of the participant’s hands. The screen and hands were viewed from a distance of approximately 80 cm through a series of 2 prisms, such that the perceived and actual direction of movement was in correspondence. Four target locations (Fig. 1*A*), indicated by open circles (1.7-cm diameter), were always visible. The distance from the start position of the fingers to the targets was approximately 10 cm. A fixation marker was presented centrally, approximately 7.8° from the sideways target locations and 4.6° from the forward target locations. Participants were instructed to maintain fixation at all times. Eye movements were not recorded during imaging. Using an identical setup, however, we confirmed outside the scanner that the task could be performed easily without eye movements.

For trials with spatial cues, the target location was indicated by illuminating the target circle. On unimanual trials 1 circle was filled and on bimanual trials 2, 1 of the left pair and 1 of the right pair. For trials with symbolic cues, an “F” or “S” (0.7° × 1°) was presented above 1 hand (unimanual trials) or both hands (bimanual trials), 1.8° lateral to fixation. For both types of cues, bimanual movements were either congruent or incongruent. Congruent trials are those in which the movements were both sideways or both forward; incongruent trials were those in which 1 movement was sideways and 1 forward (Fig. 1*A*).

Participants were instructed to make rapid reaching movements to the specified target. To measure RT in the scanner, participants were required to press 2 keys at the start of each trial, 1 with the index finger of each hand. RT was recorded as the time at which the key was released. In bimanual trials, participants were instructed to make both movements simultaneously. As a bimanual measure of RT, the average of the 2 unimanual RTs was calculated because the movement onsets for the 2 hands were closely synchronized.

An event-related design was employed. The onset of the stimulus for each reaching trial was time locked to a time repetition (TR) pulse, and the interval between successive trial onsets varied from 2.5 to 12.5 s. A scanning run consisted of 48 trials, half involving symbolic cues and half involving spatial cues. The cue type (spatial or symbolic) was maintained for 8 consecutive trials to reduce task-switching effects when changing from 1 type of cue to the other. Twelve functional runs, each containing 124 whole brain volumes (310 s) were acquired. Within each cue type, trials were pseudorandomly assigned to 1 of the 4 movement conditions (unimanual left, unimanual right, bimanual congruent, and bimanual incongruent), such that over the 12 functional runs, each cue × movement condition combination occurred 72 times. During the 0–10 s interval between trials, only the fixation cross and potential target locations were presented.

Magnetic Resonance Imaging

Imaging was performed with a General Electric Horizon echospeed whole body 1.5-T MRI scanner using a standard birdcage head coil. Head movements were minimized by using a foam pillow and padding. For functional imaging, an echo planar gradient echo imaging sequence sensitive to blood oxygenation level-dependent (BOLD) contrast was used to acquire 25 slices per TR (4.5-mm thickness, 1-mm gap), with a TR of 2.5 s, echo time (TE) of 35 ms, a flip angle of 90°, and a field of view (FOV) of 24 cm with a matrix of 64 × 64 voxels. The first 4 volumes of each functional run were discarded to allow magnetization to approach equilibrium. A high-resolution T_1-weighted axial fast spin echo sequence was used to obtain 25 slices coplanar to the BOLD images (TE = 6.3 ms, TR = 650 ms, FOV = 24 cm, matrix = 192 × 192). After all the functional runs, a high-resolution T_1-weighted image of the whole brain was acquired using a spoiled gradient-recalled 3-dimensional sequence (TR = 7.7, TE = minimum for full sampling, flip angle = 15°, FOV = 24, slice thickness = 1.2, matrix = 256 × 256 × 192).

Data Analysis

Spatial normalization and smoothing of images were carried out in SPM99 (http://www.fil.ion.ucl.ac.uk/spm). First, functional images were realigned to correct for head movement. The functional data were normalized to a standardized stereotaxic space (Montreal Neurological Institute [MNI] template provided in SPM99) and smoothed with an isotropic Gaussian kernel (8-mm full width half maximum) to give images with 25 axial slices of 2 × 2 × 2-mm voxels.

Data analysis proceeded in 2 steps. First, for each participant individually, a multiple regression, fixed-effects analysis was carried out on the data for all runs, with 1 regressor for each of the 8 conditions (2 cue types × 4 movement conditions) as well as linear regressors for each run to account for global signal changes. Each experimental trial was modeled as a short neural event at the moment of stimulus presentation (dirac delta function), convolved with a hemodynamic response function. Custom Matlab code was used to compute the percent signal change for each voxel and each condition by dividing the height (maximum – baseline) of the predicted response by the mean brightness of the voxel across the scan.

The average percent signal change estimates, 1 image per participant and condition, were then submitted to a 2nd level, mixed-effects analysis of variance, with the 8 conditions as levels of 1 factor. We then tested 3 planned comparisons: symbolically cued versus spatially cued movements (averaged over the unimanual and bimanual congruent movements), incongruent versus congruent bimanual movements for symbolic cues, and incongruent versus congruent movements for spatial cues. The error variance for the planned *t*-tests was estimated from the pooled residual variance from all conditions. The resulting statistical maps were thresholded at $t > 3.13$, $P < 0.001$, uncorrected. For this height threshold, we used a cluster-size threshold of $P = 0.05$, corrected for multiple comparisons across the whole brain. Clusterwise *P* values reflect the probability of observing a connected superthreshold region of the observed size or larger (Friston and others 1994).

Given the special role of the parietal cortex in reaching movements, we performed an additional anatomical region of interest (ROI) analysis. Spheres with the diameter of 6 mm (1 on each side) were located in the posterior dorsal superior parietal lobule (SPL) just anterior to the parietooccipital sulcus (PO) (MNI coordinates ±13, −72, 58). We also placed 3 spheres on each side along the intraparietal sulcus (IPS), resulting in posterior (±28, −72, 35), middle (32, −54, 44), and anterior (±39, −36, 44) intraparietal ROIs.

Results

Participants performed either unimanual or bimanual reaching movements in 1 of the 2 directions. The onsets of the bimanual movements were closely synchronized (mean left hand lead = 10 ms, average standard deviation = 31 ms). RTs (Fig. 1*B*) were considerably elevated when the movements were signaled by symbolic cues ($F_{1,14} = 183.34$, $P < 0.001$), for both unimanual (124 ms, effect size $d = 2.93$) and bimanual congruent (135 ms, $d = 3.75$) conditions. RTs on bimanual congruent trials for both types of cues were similar to those for corresponding unimanual trials ($F_{1,14} = 0.45$, $P = 0.51$), indicating no obligatory cost associated in planning bimanual movements.

The primary analysis focused on the congruency effect (incongruent – congruent RTs) in the bimanual trials. The congruency effect for spatial cues was 15 ms ($t_{14} = 2.92$, $P = 0.011$, $d = 0.75$). In contrast, the congruency effect for symbolic cues was an order of magnitude larger (148 ms, $t_{14} = 8.98$, $P < 0.001$, $d = 2.56$), reflected in a significant cue type × congruency interaction ($F_{1,14} = 62.75$, $P < 0.001$, $d = 2.04$). In summary, we replicated previous studies in showing that the main RT cost in planning incongruent bimanual movements arises from goal-selection processes associated with the symbolic cues. However, we also found a measurable, albeit small, influence of congruency in RT even with spatial cues (Heuer and Klein 2005), indicating a weaker effect of movement-related conflict.

Congruency Effects with Spatial Cues

In this analysis, we compared the incongruent and congruent bimanual conditions for the spatial cues only. Regions active in this comparison would be associated with conflict due to the spatial incompatibility of the target locations and/or movement directions. The small, but significant, congruency effect in the behavioral data indicates the existence of such movement-related conflict. We found clusters bilaterally in the SPL (throughout the article, we will use the anatomical term SPL to refer to the lateral convexity of the SPL dorsal to the IPS. Specifically, we refer to the posterior lateral aspects of the SPL, just anterior to the PO) in which activation was greater on incongruent than on congruent trials (Fig. 2*A* and Table 1). The activation appeared was more prominent in the right SPL. Activation within the corresponding cluster in the left SPL showed a similar trend but did not reach significance when correcting for multiple comparisons on the cluster level.

We also found a cluster of activity in the left inferior cerebellum (Crus I). The activation profile of this region (Fig. 2*C*) indicates an involvement in movement-related conflict as this region showed a congruency effect for both types of cues (Fig. 2*C*). No areas showed greater activation for congruent movements than for incongruent movements.

One possible account of the activation of SPL is that incongruent trials may have elicited more eye movements between the target locations than congruent trials. Although it is very likely that participants succeeded in keeping fixation as instructed during the task, we could not monitor eye movements in the scanner. Furthermore, activity in the SPL could also be related to covert shifts of attention between the fixation point and the 2 target locations (Serences and others 2004). Both hypotheses, however, would predict that activity in the SPL should be related to the intertarget distance on each trial. For incongruent trials, the distance between the targets was always 15.4 cm, whereas for congruent trials, this distance was either 5.5 or 22.5 cm. Although the average intertarget distance was shorter for congruent than for incongruent trials, the congruent condition with a large separation of the targets should have elicited at least as many eye movements or covert shifts of attention as the incongruent condition. To evaluate this prediction, we performed a post hoc analysis on the SPL ROI (see Materials and Methods), comparing activation for the 4 movement pairs in the spatial cueing condition. Activation levels (Fig. 3) were statistically equivalent for congruent trials involving 2 close targets (both forward) and congruent trials with spatially separated targets (both sideways) (left SPL: $t_{14} = 1.132$, $P = 0.277$; right SPL: $t_{14} = 1.55$, $P = 0.14$). Moreover, activation was greater for the mean of the 2 incongruent movement pairs compared with the spatially separated, congruent pair (left SPL: $t_{14} = 2.64$, $P = 0.019$; right SPL: $t_{14} = 3.46$, $P = 0.004$). Thus, the congruency effect in the spatial condition cannot be explained by overt or covert shifts of attention because both these processes would have predicted that the activation should have been strictly related to the intertarget distance.

Congruency Effects with Symbolic Cues

We next performed a similar analysis for the symbolic conditions, again comparing bimanual incongruent and congruent movements (Fig. 2*B* and Table 1). Regions that show a differential response in this contrast are associated with either movement-related or goal-selection conflict. The largest region

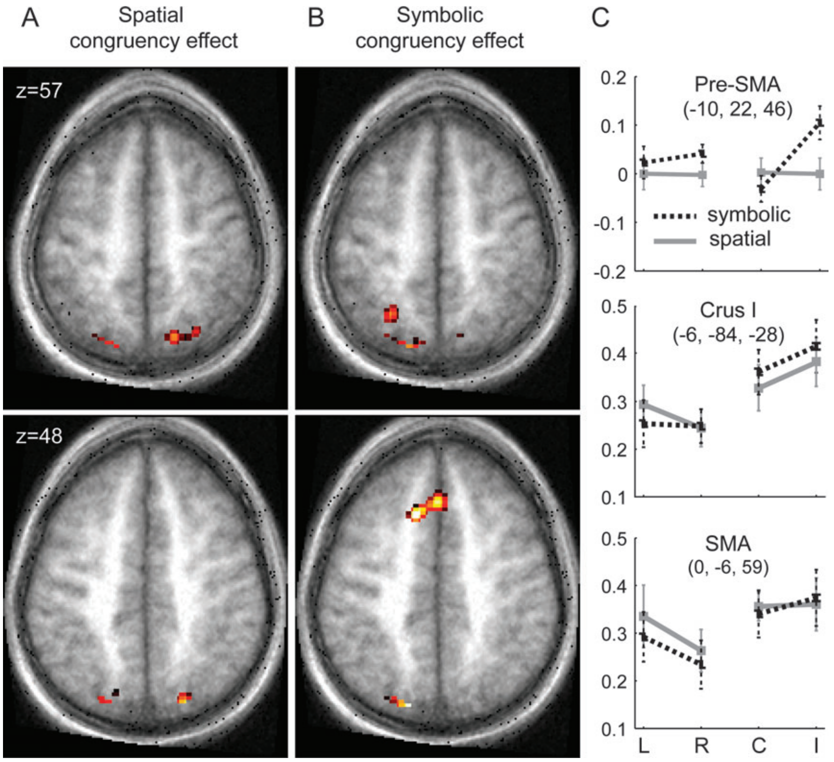

Figure 2. Cortical areas showing a congruency effect ($t > 3.13$, $P < 0.001$, uncorrected) in the (*A*) spatial and (*B*) symbolic cueing conditions. (*C*) Activity of the pre-SMA/RCZ, the left inferior cerebellum (Crus I), and the SMA relative to rest in the left unimanual (L), right unimanual (R), bimanual congruent (C), and bimanual incongruent (I), with symbolic cues (red lines) and spatial cues (blue lines).

Table 1
Regions showing a congruency effect for spatially and symbolically cued movements

Region	Side	Cluster		Voxel		MNI coordinates		
		Size (cm^3)	*P*	Peak *t*	*P* (FDR)	*x*	*y*	*z*
Congruency effect for spatial cues								
SPL[a]	L	0.61	0.066	4.12	0.347	−18	−80	54
SPL	R	1.48	0.007	4.32	0.347	10	−84	46
				4.23	0.347	16	−72	62
				3.84	0.347	28	−70	60
Inferior cerebellum (Crus I)	L	0.82	0.036	4.03	0.347	−6	−84	−28
				3.73	0.347	−12	−78	−32
Congruency effect for symbolic cues								
SPL	L	1.32	0.01	5.11	0.037	−16	−80	56
				4.31	0.079	−8	−78	56
				4.25	0.088	−16	−88	42
IPS[a]	L	0.51	0.088	3.93	0.124	−26	−60	56
SPL[a]	R	0.52	0.086	4.11	0.108	18	−78	54
				3.54	0.217	12	−74	60
Medial segment of superior frontal gyrus (pre-SMA/RCZ)	B	1.35	0.01	4.59	0.085	−10	22	46
				4.29	0.097	0	28	46

Note: Height threshold was $t = 3.13$, $P = 0.001$ (uncorrected), and the smoothness was 11.5-mm full width half maximum. The search volume encompassed the whole brain (1502.3 cm^3). For each cluster, we report the side (L, left; R, right; B, both) and *P* value (corrected for multiple comparisons over the whole brain) of observing a cluster of that size or larger. For each local maximum within the clusters, the *t* value, the corrected false discovery rate (FDR), and the location in MNI coordinates are reported.
[a] Regions showed only a statistical trend on a clusterwise level ($P < 0.1$).

was in the left SPL. Two smaller clusters, 1 in the left IPS and the other in the right SPL, were not significant on a clusterwise level. These 3 parietal areas overlapped with the regions sensitive to the congruency contrast for spatial cues, suggesting involvement in movement-related conflict. The hemispheric asymmetry, however, was reversed. For spatial cues the congruency effect in the right SPL was significant, whereas for symbolic cues the effect was only significant in the left SPL. In both cases, the corresponding region in the other hemisphere showed a similar trend that failed to reach significance.

The 4th region activated in this contrast was the medial segment of the superior frontal gyrus, involving pre-SMA and extending into the rostral cingulate zone (RCZ) (Picard and Strick 2001). Two maxima were found, one along the midline and the second in the left hemisphere. This region showed increased activation only for incongruent symbolic stimuli; no

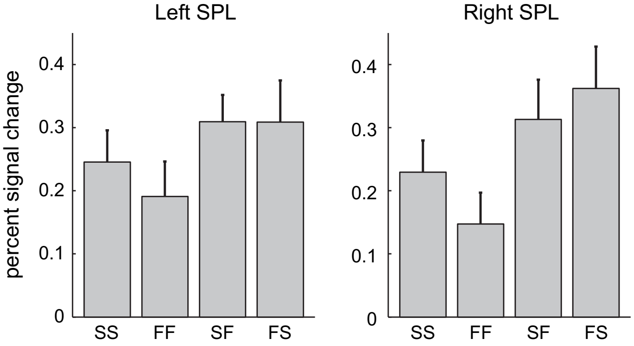

Figure 3. Activity in the left and right SPL in the bimanual conditions using spatial cues. Results are presented for congruent movements, sideways–sideways (SS), forward–forward (FF), and incongruent movements (SF and FS). The increase in activation for the incongruent conditions was observed even when compared with the SS condition in which the 2 targets were spatially distant from each other.

difference was found in the same contrast for spatial cues (Fig. 2*C*), resulting in a significant cue by congruency interaction, $t_{14} = 2.52$, $P = 0.012$. Indeed, when compared with the rest, the pre-SMA region was only activated in the symbolic incongruent condition. This result strongly suggests that activation here is related to conflict associated with goal selection.

To test whether other regions would show goal-selection conflict, we also calculated a mapwise cue × congruency interaction contrast, masked by areas that showed a congruency effect when averaging over spatial and symbolic cues. The only sizeable region was located in pre-SMA, although even here the activation level was not significant when correcting for multiple comparisons ($P = 0.22$). The opposite interaction contrast (stronger congruency effect during spatially cued than during symbolically cued movements) did not reveal any regions.

No Congruency-Related Activity in SMA

No congruency-related activity was found in the SMA proper, even when we pooled the results of the spatial and symbolic condition and lowered the threshold to $P < 0.05$, uncorrected. This null finding is surprising, given the large number of imaging studies suggesting a special role for this region in resolving conflict associated with bimanual coordination (Sadato and others 1997; Jäncke and others 2000; Debaere and others 2001; Steyvers and others 2003). To further examine activation in SMA, we placed a spherical ROI of 6-mm diameter at the peak of task-related SMA activity (MNI 0, –6, 59; Fig. 2*C*). The effect of congruency was not significant, $t_{14} = 0.84$, $P = 0.23$. Thus, for our task, we found no evidence that SMA was activated by bimanual conflict. Furthermore, activity in the bimanual congruent conditions was not greater than that in the left unimanual condition ($t_{14} = 1.23$, $P = 0.23$), indicating that the SMA also was not activated during bimanual movements in general.

Areas Involved in Symbolic Translation

To identify the neural correlates associated with the translation of symbolic cues to responses, we used the contrast symbolic > spatial, averaged over the left unimanual, right unimanual, and bimanual congruent conditions. We excluded the bimanual incongruent condition to focus on processes involved in symbolic translation in the absence of goal-selection conflict. This contrast (Fig. 4 and Table 2) revealed an elongated region along the left IPS that extended into the posterior SPL. Two other left hemisphere regions, ventral premotor cortex and inferior frontal gyrus, also showed more activity for reaches cued symbolically than movements cued spatially. Thus, apart from bilateral activity in visual areas, we found a strong left lateralization for movements requiring symbolic translation. This lateralization pattern was evident even when participants used their nondominant left hand to perform the movements, although to a lesser degree.

Parietal ROI Analysis

The parietal lobe showed a complicated pattern of activation, sensitive to cue type, congruency, and their interaction. To examine these effects in detail, we placed 3 spheres with a radius of 6 mm and a center-to-center distance of 20 mm along the left and right IPS, respectively, plus equally sized spheres bilaterally in dorsal posterior SPL near the crown of the parietal cortex, just anterior to the parietal–occipital sulcus (see Materials and Methods, Fig. 5). The placement of the ROIs was designed to follow the main swathe of task-related activity (all movements vs. rest) in the parietal cortex. The center of the spheres in the IPS was located on the dorsal bank; however, the ROIs may have included activity from the ventral bank due to smoothing and anatomical variability. Although many open questions concerning the functional organization of the posterior parietal cortex in humans remain, recent evidence (for a review, see Culham and Kanwisher 2001) would indicate that our posterior ROI in the IPS included area V7, the middle ROI possible functional equivalents of the lateral and ventral intraparietal area (see also Schluppeck and others 2005), and the anterior ROI parts of the anterior intraparietal area and area 5. The ROI in the dorsal SPL included area PO and other parts of the parietal reach region (Connolly and others 2003). For each anatomically defined region, we performed a set of 1-sided planned *t*-tests and adjusted the individual threshold to $P < 0.00625$ using Bonferroni correction, such that the chance of the overall type I error was $P < 0.05$ for each contrast.

First, we compared left and right unimanual trials, averaged across spatial and symbolic cues, to determine whether the movement-related activity was specific to movements of the contralateral limb or whether it lacked effector specificity. From all ROIs, only the left anterior IPS, $t_{14} = 3.00$, $P = 0.005$, showed greater activation for contralateral than for ipsilateral movements, although the right anterior IPS approached significance, $t_{14} = 2.57$, $P = 0.011$. All other parietal ROIs showed similar activation for left- and right-hand movements, indicating limb-independent contributions to reaching.

We then tested whether parietal regions showed higher activity during symbolically versus spatially cued movements. Consistent with the left lateralization in the mapwise contrast, we found greater activation for symbolic movements in the left middle ($t_{14} = 3.79$, $P < 0.001$) and posterior IPS ($t_{14} = 3.28$, $P < 0.001$) but not in the homologous right hemisphere ROIs. There was also a trend of increased activity for symbolically cued movements in the SPL (left: $t_{14} = 2.65$, $P = 0.018$; right: $t_{14} = 2.41$, $P = 0.030$).

Finally, we tested the congruency effect, averaged over symbolic and spatial cues. The effect was pronounced in the posterior SPL (left: $t_{14} = 3.89$, $P < 0.001$; right: $t_{14} = 4.02$, $P < 0.001$). A similar trend in the right and left posterior IPS failed to reach significance. None of the ROIs showed a reliable cue × congruency interaction, although we found a trend toward an interaction in the left middle IPS, $t_{14} = 2.22$, $P = 0.021$.

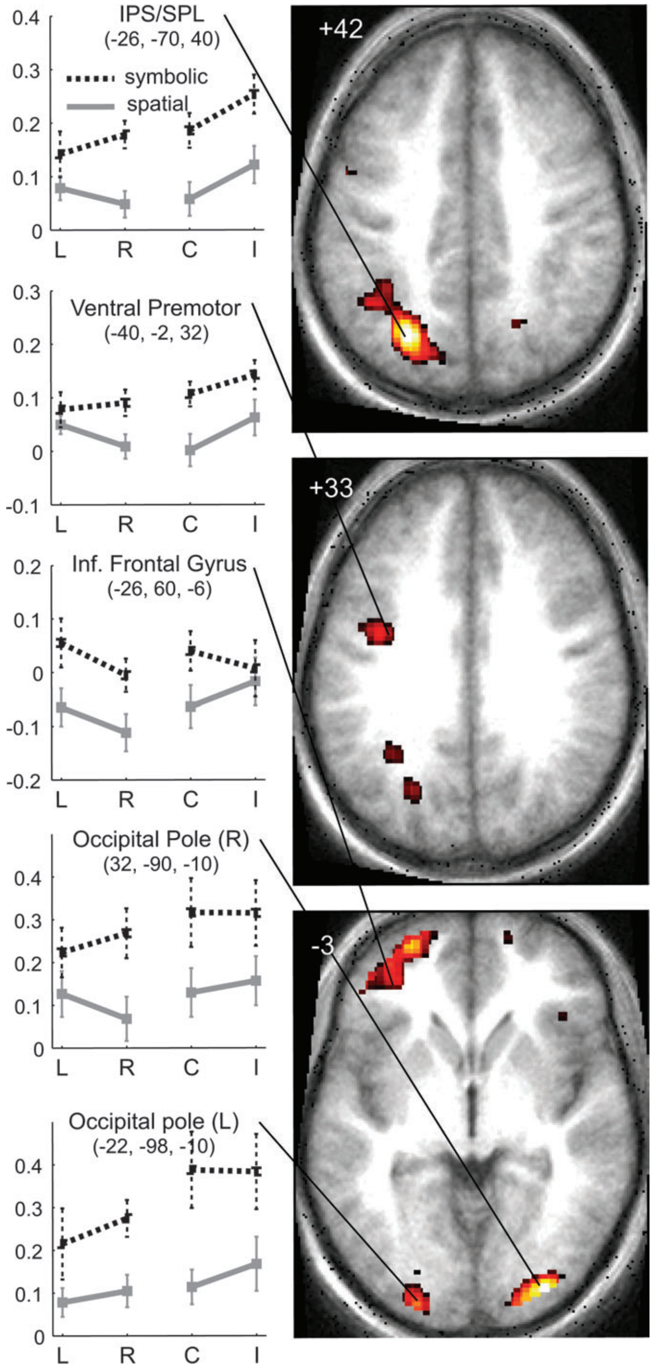

Figure 4. Areas showing greater activity for symbolically cued movements than for spatially cued movements ($t > 3.13$, $P < 0.001$, uncorrected), averaged across the left unimanual (L), right unimanual (R), and bimanual congruent (C) trials. Line plots show percent signal change relative to baseline for symbolic cues (red lines) and spatial cues (blue lines) in ROIs of diameter 6 mm centered on the local maxima of the statistical map. MNI coordinates of centers are given in parentheses. The results for the bimanual incongruent condition (I) are not included in the contrast but are shown in the line graphs.

In sum, we observed 3 functional gradients in parietal cortex. We found effector-specific activity in the anterior IPS, indicating processes related to limb-specific motor programming and/or execution. Posterior aspects were equally active whether the left or right hand was used. Second, we observed a clear left lateralization of processes related to symbolic cues, mostly in the middle and posterior IPS. Finally, an effect related to the congruency was found bilaterally in the posterior SPL.

Discussion

Bimanual coordination has proven to be a fertile area of study for exploring constraints underlying motor control and skill. By comparing conditions in which either symbolic or spatial cues were used to indicate the requisite movements, 2 distinct sources of constraint can be identified. One source arises when 2 conflicting symbolic stimuli have to be translated into movement goals for the 2 hands. This goal-selection conflict leads to a strong increase in RT (Diedrichsen and others 2003; Hazeltine and others 2003), a result replicated in the current study. We have argued (Ivry and others 2004) that this source is not specific to motor control but rather reflects a general feature of our cognitive architecture, being similar to conflict-related processes identified in a wide range of tasks (e.g., Eriksen BA and Eriksen CW 1974; MacLeod 1991; Ivry and others 1998). The second source is more specific to the motor system, reflecting a preference to produce movements that involve symmetric target locations and symmetric movement paths and/or engage homologous muscles (Swinnen 2002; Carson 2005).

Movement-Related Conflict in Superior Parietal Cortex and Inferior Cerebellum

Activation related to congruency was found in the posterior SPL and the left inferior cerebellum. The similarity of this effect for spatial and symbolic cues suggests that it reflects cross talk of processes related to motor planning and execution. This result is consistent with a recent study showing activation in superior parietal areas for bimanual movements that are incongruent either because the movements are along nonparallel trajectories or because they require unequal amplitudes (Wenderoth and others 2005). A parietal locus of movement-related conflict is also supported by the observation that posterior, but not anterior, commisurectomy led to a reduction in spatial coupling during bimanual movements (Eliassen and others 1999). Unlike the left hemisphere bias for the symbolic conditions, the posterior SPL activation for spatial cues was right lateralized (see also Wenderoth and others 2004).

What processes in incongruent trials lead to the activation of the posterior SPL? The posterior SPL represents target locations in retinocentric, rather than in hand-centered coordinates (Medendorp and others 2003). Moreover, this region is engaged when a target is displaced during a reaching movement, whereas more anterior parietal regions (area 5) are activated when movement kinematics are altered (Diedrichsen and others 2005). This suggests that representations in the posterior SPL are not related to movement parameters per se but rather to the spatial goals of movements. On congruent trials, participants can exploit a preference to produce mirror-symmetric movements, demanding attention only to one of the target locations. The lack of symmetry for incongruent targets likely requires a more complex spatial representation and increased demands in monitoring movements to these positions.

SMA: Specialization for Bimanual Movements or Temporal Coordination?

In previous studies, SMA proper (Picard and Strick 2001) has been found to be consistently activated during incongruent bimanual compared with either unimanual or congruent

Table 2

Regions showing a higher BOLD signal for symbolically cued movements compared with spatially cued movements

Region	Side	Cluster		Voxel		MNI coordinates		
		Size (cm^3)	*P*	Peak *t*	*P* (FDR)	*x*	*y*	*z*
IPS/SPL	L	8.51	<0.001	6.58	<0.001	−26	−70	40
				4.22	0.004	−36	−50	38
Middle frontal gyrus	L	5.06	<0.001	5.39	<0.001	−26	60	−6
				5.05	<0.001	−32	44	−12
				4.57	0.001	−36	52	−6
Precentral gyrus (ventral premotor)	L	1.64	0.005	4.11	0.006	−40	−2	32
				3.74	0.015	−50	2	38
Occipital pole	R	3.26	<0.001	6.31	<0.001	32	−90	−10
				3.62	0.02	38	−78	−18
Occipital pole	L	4.60	<0.001	5.98	<0.001	−22	−98	−10
				3.93	0.009	−28	−88	−29

Note: Parameters as in Table 1.

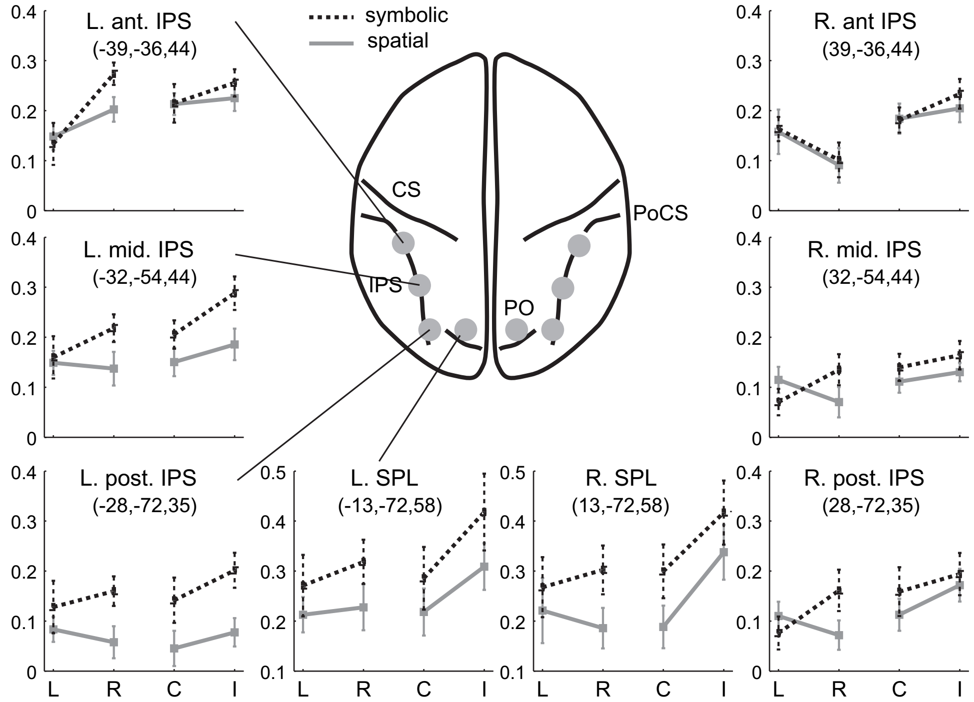

Figure 5. Percent signal change for 8 ROIs, placed along the IPS and in the posterior SPL in the left and right hemispheres. Left unimanual (L), right unimanual (R), bimanual congruent (C), and bimanual incongruent (I) movements cued symbolically (red lines) or spatially (blue lines). CS, central sulcus; PoCS, postcentral sulcus.

bimanual movements (Sadato and others 1997; Jäncke and others 2000; Debaere and others 2001; Steyvers and others 2003). These findings, together with lesion studies (Brinkman 1984), have led to the hypothesis that SMA is an area specialized for bimanual coordination. Our finding that SMA activity did not increase during incongruent movements for either spatial or symbolic cues is at odds with this hypothesis. In fact, SMA activation was no greater during bimanual movements than during unimanual movements performed by the left hand, challenging the notion that SMA plays a special role in bimanual coordination.

An alternative conceptualization of SMA function is further motivated by evidence showing that this region is engaged during the production of “unimanual” asynergistic movements (Ehrsson and others 2002) or offbeat synchronization with a train of external stimuli (Oullier and others 2005). Interestingly, these studies, as well as those showing SMA activation during bimanual movements (Sadato and others 1997; Jäncke and others 2000; Debaere and others 2001; Wenderoth and others 2004), have all involved repetitive movements. In contrast, in our study, the participants made discrete, goal-directed reaching movements. Taken together, the current evidence suggests that the SMA may not be specialized for bimanual movements per se but that its engagement may be dictated by 1 of the 2, nonexclusive, factors. First, SMA may be recruited during repetitive movements due to the temporal or sequential aspects of coordination (Lewis and others 2004), processes minimally required during discrete movements. Second, the SMA may be recruited when the movements are based on internal representations of the movement goals as is commonly required in studies of repetitive movements, compared with conditions in which the movements are directed to external, visual targets (Goldberg 1985). Although further work is needed to exactly describe the functional role of the SMA in coordination, our results suggest that this role is likely to be similar for both unimanual and bimanual movements.

Goal-Selection Conflict in Medial Frontal Cortex

Conflict-related activity in the pre-SMA and RCZ was specific to the symbolic cueing conditions. This contrasts with parietal areas in which activity in incongruent trials was increased with either spatial or symbolic cues. Furthermore, activity in medial frontal regions was not elevated above the resting baseline on unimanual trials or bimanual trials involving congruent movements, whereas parietal areas were involved in the production of these movements. Thus, activation of medial frontal areas was restricted to situations when multiple response alternatives compete, consistent with the extensive literature on the pre-SMA (Botvinick and others 2004; Nachev and others 2005; Rushworth and others 2005). These studies have typically involved single movements, and the conflict reflects competition among different response codes (e.g., colors or color names in Stroop task, MacDonald and others 2000) or between making a response and withholding a response (e.g., go–nogo tasks, Garavan and others 2003).

The current study suggests that a similar source of conflict arises when planning bimanual movements based on symbolic cues. For example, when participants are confronted with a mixed stimulus such as "SF," they must link these cues to their associated responses and decide whether to move the right hand forward and the left hand sideways or the left hand forward and the right hand sideways. Thus, response conflict here entails an "assignment problem" (Diedrichsen and others 2003) during goal selection. In contrast, this form of conflict is not present when the symbolic cues indicate congruent movements. For example, for the stimulus "SS," a sideways trajectory can be assigned to each hand.

In a recent study, Wenderoth and others (2005) reported activity in cingulate motor areas during repetitive bimanual movements in which the amplitude of right-hand movements changed every 3.3 s, whereas the amplitude of the left hand remained constant. Although the authors argued that the increase was specific to reprogramming the movement amplitude, our findings suggest an alternative hypothesis: activity in the pre-SMA may reflect goal-selection conflict that arose each time a switch of the movement amplitude required (re)solving the assignment problem.

It is noteworthy that the pre-SMA/cingulate region did not show increased activity during incongruent, spatially cued movements. Consistent with the minimal RT cost with spatial cues, the results indicate that goal-selection conflict does not arise when movement goals are directly specified.

Symbolic Processing and a Left-Lateralized Network

We identified a left-lateralized network involved in translating symbolic cues to actions. It consisted of left IPS/SPL, left ventral premotor cortex, and left inferior frontal cortex. Whereas this pattern of lateralization may be related to the linguistic nature of the stimuli, studies using nonlinguistic stimuli have implicated the same left parietal–premotor network in the translation of arbitrary stimuli to actions (Deiber and others 1991; Hazeltine and others 1997; Schluter and others 2001; Rushworth and others 2003).

The left lateralization for processing the symbolic cues may be part of a more general left hemisphere specialization for skilled movements and tool use (Johnson-Frey and others 2005). Ideomotor apraxia, a deficit in performing skilled complex movements based on imitation or symbolic cues, is associated with lesions in the left middle frontal gyrus, left inferior parietal cortex, and left IPS (Haaland and others 2000). The network that we identified as associated with symbolic translation overlaps considerably with these regions in premotor and parietal cortex but also appears to extend more posterior along the IPS and further into the SPL. Therefore, it also includes parts of the "dorsal–medial" stream (Rizzolatti and Matelli 2003), a group of functionally related areas that contain the parietal reach region (Snyder and others 2000; Connolly and others 2003).

The strong left lateralization of the network related to action selection based on symbolic cues may lead to a bottleneck during bimanual trials when 2 nonidentical cues have to be associated with their respective target locations. Following this hypothesis, goal-selection conflict occurs within the processing stream normally involved in the selection of movements based on symbolic stimuli. Consistent with this idea, the congruency effect in the symbolic condition was more pronounced in the left hemisphere and extended ventrally and laterally into the left IPS. These areas overlap considerably with left parietal regions involved in the translation of symbolic stimuli. Although these results suggest that goal-selection conflict arises from processes in the left parietal cortex, these findings are far from conclusive. Both incongruent symbolic and spatial cues led to conflict-related activity in the SPL, indicating that much of the activity here reflected movement-related conflict. In contrast to the left parietal cortex, medial frontal areas were not involved in symbolic processing on unimanual or bimanual congruent trials but were only activated in the incongruent symbolic condition. Thus, it would appear that the medial frontal regions are specifically engaged when conflict between competing response alternatives arises.

Summary

Our results indicate that limitations during bimanual movements result from 2 behaviorally and neurally distinct mechanisms. Movement-related conflict, as isolated in the spatial cueing conditions, led to a small increase in initiation time but strongly increased activity in the posterior SPL. SPL activation was also greater for incongruent movements that were symbolically cued, consistent with the idea that movement-related conflict should be independent of the manner in which the actions are cued. We attribute this activation to additional processes involved in planning and monitoring the asymmetric bimanual movements. Behaviorally, the preference to produce symmetric actions can be overcome very efficiently during goal-directed reaching movements (see also Diedrichsen and others 2004). In contrast, with symbolic cues, a large cost in RT is observed on incongruent trials, together with activation of the pre-SMA and cingulate motor areas. We attribute this medial frontal activation to processes involved in conflict that arises during goal assignment and suggest that this form of conflict is not present with spatial cues because the goals for each hand are directly specified. Together, the results suggest that bimanual movements may be difficult because of a cognitive limitation in selecting what to do with each hand and a limitation of the motor system in planning how to do so.

Notes

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