

Neural Systems Underlying Observation of Humanly Impossible Movements: An fMRI Study

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Previous studies have indicated that largely overlapping parts of a complex, mainly fronto-parietal, neural network are activated during both observation and execution of an action. If these two processes are inextricably linked, increases of neural activity contingent upon action observation should be found only for movements that can actually be performed. Using functional magnetic resonance imaging, we investigated whether observation of possible and biomechanically impossible movements of fingers activated the same neural systems. Thirteen healthy subjects were scanned during observation of video-clips showing abduction/adduction movements of the right index or the little finger, which were defined as biomechanically possible or impossible according to the range of their angular displacement at the metacarpo-phalangeal joint. The mere observation of possible and impossible hand movements induced a selective activation of left precentral and left inferior frontal regions, thus indicating that motor-related areas map body actions even when they violate the constraints of human anatomy. An increase of the blood oxygen level-dependent signal selectively linked to observation of impossible hand movements was found in sensorimotor parietal regions. Our results suggest that while premotor areas code human actions regardless of whether they are biologically possible or impossible, sensorimotor parietal regions may be important for coding the plausibility of actions.

Keywords: action observation, body image, fMRI, impossible human movements, mirror neurons, moving objects

Introduction

Recent neurophysiological studies in awake monkeys have shown that neurons in cortical frontal areas are not only activated during execution and planning of actions but also during observation of actions performed by other individuals (Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996a; di Pellegrino *et al.*, 1992). The discovery of these visuomotor neurons, called 'mirror neurons', radically changed the notion of completely separate neural substrates for sensory and motor processing. Thus, perception and action may rely upon observation-execution matching systems (Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996a; di Pellegrino *et al.*, 1992), which can play a crucial role in both imitative and non-imitative action learning (Rizzolatti *et al.*, 1996b, 2001).

Neuroimaging (Grafton *et al.*, 1996; Rizzolatti *et al.*, 1996b; Grezes *et al.*, 1999, 1998) and neurophysiological (Fadiga *et al.*, 1995; Cochin *et al.*, 1999; Hari *et al.*, 1998) studies in humans indicate that neural structures known to be involved in action execution become active during action observation. This link is further supported by behavioral studies showing that execution of a given action is positively or negatively modulated by observation of the same or a different action (Brass *et al.*, 2001; Craighero *et al.*, 2002).

In keeping with this view is evidence from transcranial magnetic stimulation and magnetoencephalographic studies that motor facilitation induced by observation is greater for natural than unnatural hand orientations (Maeda *et al.*, 2002) and for live rather than video acts (Jarvelainen *et al.*, 2001). Moreover, while observation of actions performed by a virtual hand activates only lateral occipital cortices, observation of actions performed by a real hand activates a visuospatial network involved in action representation and execution (Perani *et al.*, 2001). In the same vein, observation of a grasping action performed by a human model elicits neural activity in the premotor cortex. By contrast, no comparable activation was found during observation of the same action performed by a robotic arm (Tai *et al.*, 2004). Furthermore, execution of an arm movement was interfered with by observation of incongruent movements performed by another human individual but not by observation of incongruent movements performed by a robotic arm (Kilner *et al.*, 2003). Finally, it has also been suggested that only observation of actions belonging in the motor repertoire can be mapped onto the observer's motor system (Buccino *et al.*, 2004a).

Relevant to the present research is whether humans can do what they see. Indeed, humans can 'conceive' movements they cannot perform such as actions they have never learned, e.g. very complex acrobatic exercises or impeccable tennis serves. In principle, actions that cannot be performed can be learned through practice. Indeed, young children cannot perform several types of movement until learning is completed. However, it is also possible to try and imagine movements that could never be performed because of the constraints of human anatomy. Obviously, in daily life we never observe impossible actions such as walking upside down.

By using functional magnetic resonance imaging (fMRI), we sought to determine the pattern of neural activity evoked by observation of biomechanically impossible, articulated finger movements. We reasoned that if the mirror-matching system is strictly linked to execution, it should not be activated during observation of actions that cannot be performed. Thus, the main aim of the present study was to explore whether a different set of areas is activated during the observation of possible and impossible hand movements. We also checked whether different patterns of activation were specific for human movements by testing the effect of observing naturalistic or impossible movements of scissors blades, which were used as a non-corporeal control.

Materials and Methods

Participants

Thirteen healthy subjects (one male; mean age = 24 years, range = 20-29 years) took part in the experiment. Eleven subjects were right-handed

(11 female) and two were left-handed (one female) according to a standard handedness inventory (Oldfield, 1971). All subjects had normal or corrected-to-normal vision. They gave their written consent to participate to the study and were paid for their participation. All subjects were naive as to the purpose of the experiment. The study was approved by the Ethics Committee of the University of Chieti 'G. D'Annunzio'.

Stimuli and Procedure

The experimental stimuli consisted of video-clips depicting two categories of moving stimuli, namely abduction-adduction movements of the index or little finger of the right hand (body movement), and the sliding of scissors blades (non-body movement). We also showed both corporeal and non-corporeal stimuli as static objects. Based on the range of angular joint displacements, finger movements were defined as biomechanically possible or impossible. In a similar vein, based on the direction of blade sliding, scissors movements were defined as mechanically possible or impossible (Fig. 1). We chose stimuli with comparable perceptual complexity. Angular displacement and movement rate, which are by and large the two most important variables to control for, were matched. The influence of low-level variables, such as color and brightness, was minimized at the analysis stage by comparing the observation of moving hands and scissors to the respective static images. The starting position of the impossible hand movements was designed so as to induce a sensation of joint stretch and to avoid any ambiguity about the biomechanical impossibility of the movement.

Stimuli were projected onto a back-projection screen situated behind the subject's head and were visible in a mirror (10 × 15 cm).

Video-clips were shown in 13 s blocks (see Fig. 1), with 6 s fixation periods between blocks. Each block comprised three short video-clips belonging to one of the six stimulus categories (possible finger or scissors movement; impossible finger or scissors movement; static finger or scissors). The different blocks were alternated in a fixed sequence, with each category presented three times during each experimental session. Each subject underwent two consecutive experimental sessions.

Subjects were asked to simply observe the video-clips in free vision. They were informed that at the end of the experimental sessions questions would be asked about the images and the possible sensations evoked by each category of observed stimuli.

After fMRI acquisition, subjects were presented with videos of moving body and non-body stimuli and asked to specify whether the movies induced any aversion effect or somatic feelings such as pain or joint stretch. We used a seven-point Likert scale. A score of 0 indicated no effect (no aversion or no somatic feelings), and a score of 6 maximal effect (very high aversion and very vivid somatic feelings).

MRI Acquisition and Data Analysis

All images were collected with a 1.5 T Siemens Magnetom Vision scanner with a standard head coil operating at ITAB (Chieti, Italy). T_1 -weighted anatomical images were collected using Siemens multiplanar rapid acquisition gradient echo sequence (1 mm isotropic voxels, 160 sagittal slices, $T_R = 11.4$ ms, $T_E = 4.4$ ms). Functional images were collected with

a gradient echo EPI sequence. Each experimental session included 117 consecutive volumes comprising 24 consecutive 4 mm thick slices oriented parallel to the anterior-posterior commissure plane and covering the whole brain ($T_R = 3$ s, $T_E = 60$ ms, 64×64 image matrix, 4×4 mm in-plane resolution).

fMRI data were analyzed using SPM2 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London) according to the following procedure. For each subject, functional images were first corrected for head movements using a least-squares approach and six-parameter rigid body spatial transformations (Friston *et al.*, 1995). The high-resolution anatomical image and the functional images were then stereotactically normalized to the Montreal Neurological Institute (MNI) brain template used in SPM2 (Mazziotta *et al.*, 1995). Functional images were resampled with a voxel size of $4 \times 4 \times 4$ mm and spatially smoothed with a three-dimensional Gaussian filter of 6 mm full width at half maximum to accommodate anatomical variations between subjects (Friston *et al.*, 1995). Images were subsequently analyzed using a random effect approach. The time series of functional MR images obtained from each participant were analyzed separately. The effects of the experimental paradigm were estimated on a voxel-by-voxel basis using the principles of the general linear model, extended to allow the analysis of fMRI data as a time series (Worsley and Friston, 1995). Low-frequency noise was removed with a high-pass filter (time constant 128 s). Each experimental block was modeled using a boxcar, convolved with a canonical hemodynamic response function, chosen to represent the relationship between neuronal activation and blood flow changes. These single-subject models were used to compute six contrast images per subject, each representing the estimated amplitude of the hemodynamic response in each observation condition relative to the fixation baseline. Contrast images from all subjects were entered into a group repeated-measures analysis of variance with non-sphericity correction as implemented in SPM2 (Worsley and Friston, 1995; Frackowiak *et al.*, 2003). The statistical threshold was $P < 0.05$, corrected for multiple comparisons using false discovery rate (FDR). Instead of controlling the chance of *any* false positives (as Bonferroni or random field methods do), FDR controls the expected *proportion* of false positives among suprathreshold voxels. An FDR threshold is determined from the observed P -value distribution, and hence is adaptive to the amount of signal in the data. FDR has become increasingly popular in neuroimaging research since it is generally more sensitive than traditional methods (Genovese *et al.*, 2002; Nichols and Hayasaka, 2003).

We first identified regions showing significant activation during observation of each of the four movement conditions (possible hand, impossible hand, possible scissors and impossible scissors) with respect to observation of the respective static object. We then limited our interest to regions activated by any of these movement conditions and systematically looked at differential activation effects occurring there by comparing different object types (finger versus scissors) and different movement types (possible versus impossible). For these differential effects, we used a region of interest (ROI) including all voxels activated by at least one of the four movement conditions. Correction of multiple comparisons was computed for the overall ROI volume. We also explored

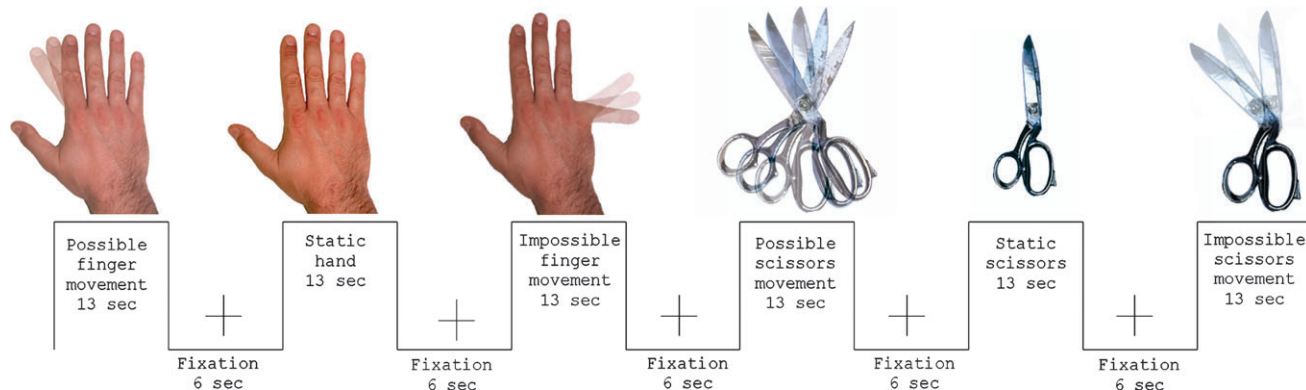


Figure 1. Selected superimposed frames from the video sequences of finger movements and blade sliding and time series of the different observation blocks.

differential effects outside the ROI, using correction for multiple comparisons over the overall brain volume outside the ROI. To test for the effect of object type (hand versus scissors), we performed the two-tailed contrasts [(possible hand movement - static hand) - (possible scissors movement - still scissors)] and [(impossible hand movement - static hand) - (impossible scissors movement - static scissors)]. To test for the effect of movement type (possible versus impossible), we performed the two-tailed contrasts (impossible hand movement - possible hand movement) and (impossible scissors movement - possible scissors movement).

Results

Neural Mapping of Moving Fingers and Scissors

Passive observation of each of four types of movement relative to observation of the respective static object activated a wide and partially overlapping bilateral network of occipito-temporal areas (see Fig. 2).

Frontal activation was observed only during observation of moving body parts and not of moving non-body objects. It encompassed the inferior frontal gyrus (pars opercularis) and precentral gyri bilaterally.

Parietal activation was found for both body and non-body objects in the superior postcentral gyrus bilaterally and in the superior parietal lobe, while the inferior part of the postcentral gyrus and the supramarginal gyrus bilaterally was predominantly or exclusively activated by observation of moving corporeal stimuli. Finally, a significant increase of the BOLD signal in the left posterior thalamus was found only during observation of possible hand movements.

Comparison of Moving Fingers versus Moving Scissors

We searched in the above-described areas for regions that were differentially activated by body (finger) versus non-body (scissors) movements (see Materials and Methods for contrast

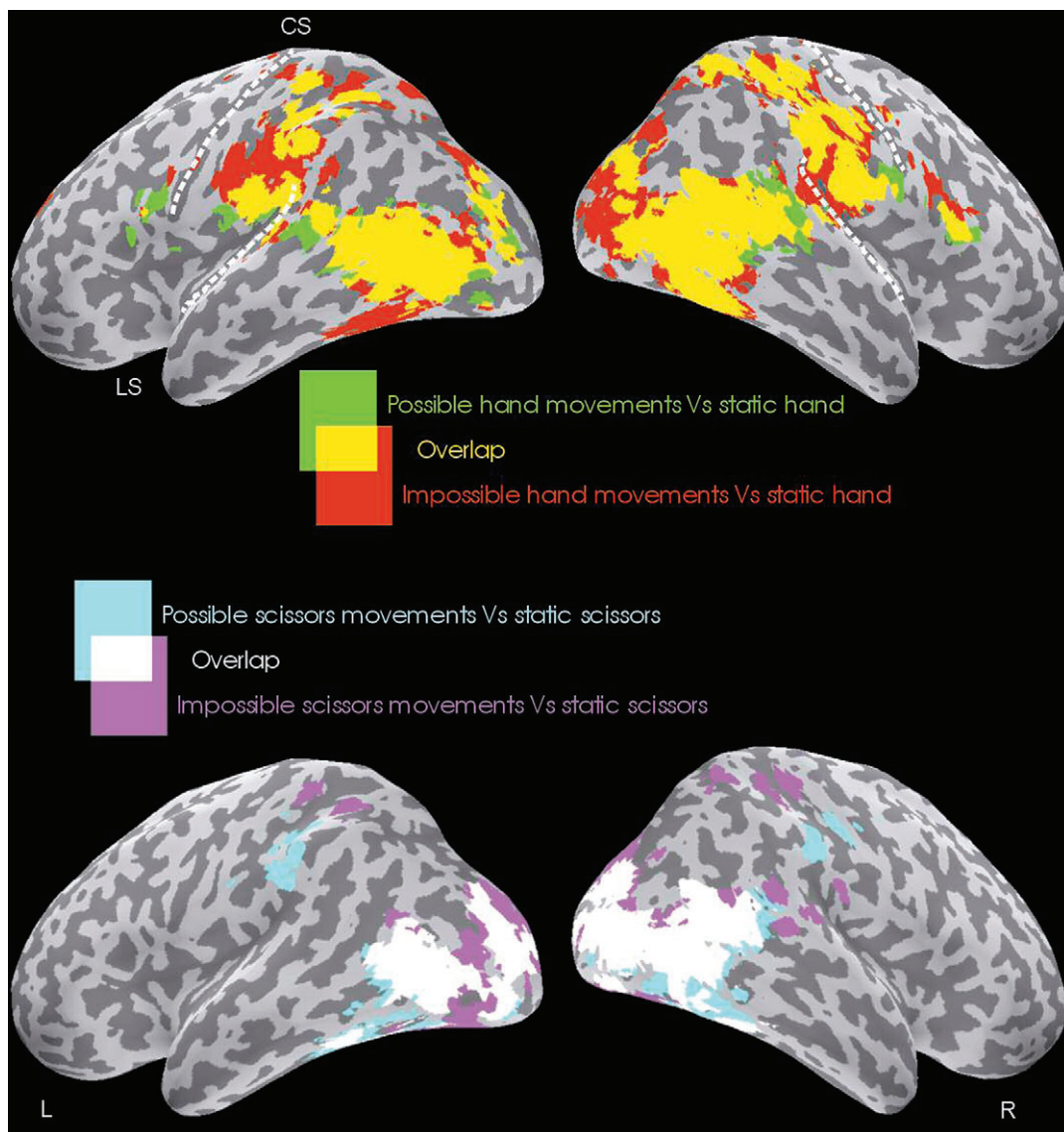


Figure 2. Upper part: Regions activated during observation of possible hand movements (green) and impossible hand movements (red) relative to observation of static hands. Yellow areas indicate regions of overlap. Lower part: Regions activated during observation of possible scissors movements (cyan) and impossible scissors movements (magenta) relative to observation of static scissors. White areas indicate regions of overlap. Group activation data are rendered on the reconstructed and unfolded cortical surface of a 'canonical' brain (Mazziotta *et al.*, 1995).

specification). For possible movements, we found more activation for finger than for scissors movement observation in the left inferior frontal gyrus, the inferior parietal lobule bilaterally, the right superior postcentral gyrus, and the bilateral middle temporal gyrus. Interestingly, a significant increase of the blood oxygen level dependent (BOLD) signal was also found in the left posterior thalamus (Table 1a; Fig. 3, green and yellow patches). No regions were significantly more active for possible scissors than possible hand movements.

Activation was higher for impossible finger than impossible scissors movements in the precentral and supramarginal gyri bilaterally, the right superior parietal lobe, and the bilateral occipito-temporal cortex (Table 1b; Fig. 3c, red and yellow patches). Again, no region showed more activation for impossible scissors than for impossible hand movements.

Comparison of Possible versus Impossible Movements

Finally, when we compared possible and impossible movements, we found that no single voxel showing a reliable activation for moving versus static body and non-body objects was influenced by whether the scissors movements were possible or impossible. Conversely, within our ROIs four distinct clusters of voxels showed higher activity during observation of impossible than possible hand movements (Table 2 and Fig. 4). The largest cluster was centered around the right supramarginal gyrus and extended into the right postcentral gyrus. A second cluster was symmetrically located in the left parietal lobe and included the supramarginal and postcentral gyri. The left-sided cluster was much smaller than the right one (63 versus 147 voxels). These posterior parietal cortex (PPC) activations were

centered in the inferior aspect of PPC (Brodmann's area 40) and extended into the superior posterior aspect of PPC (Brodmann's area 7).

The other two clusters involved parts of temporo-occipital areas. Again, the activation was much greater in the right hemisphere (127 versus 12 voxels). The temporo-occipital cluster of activation reported here was located near the so-called extrastriate body area (EBA), a cortical region that seems to be specifically involved in the analysis of non facial body parts (Downing *et al.*, 2001; Urgesi *et al.*, 2004).

Previous PET studies reported a predominantly right-sided cluster of temporo-occipital activation during perception of actions (Decety *et al.*, 1997; Grezes *et al.*, 1998).

Differential Effects Outside the ROI

When we searched for differential activation outside the ROI, defined as the set of regions activated by either type of moving stimulus relative to the respective static image, we found no effect of either object type (hand versus scissors) or movement type (possible versus impossible) in any brain region.

Subjective Reports

Impossible hand movements were judged as significantly more aversive than possible hand movements (mean \pm SE: 3.26 ± 0.82 versus 0.44 ± 0.41 ; $P < 0.01$). In a similar vein, impossible hand movements induced joint stretch feelings in the observer more often than possible hand movements (3.07 ± 0.79 versus 0.70 ± 0.46 ; $P < 0.01$). Neither possible nor impossible scissors movements induced any consistent aversion or other feelings in the observer.

Discussion

We explored the neural systems recruited during observation of articulated movements of body parts (abduction-adduction movements of the index or little finger) and intrinsic movements of man-made objects (the sliding blades of a pair of scissors). The observed body movements were either easily executable or non-executable because they clearly violated the biomechanical constraints of human anatomy. In a similar vein, the observed tool movements were either naturally or unnaturally articulated. More explicitly, while possible finger and scissors movements can be observed in daily life, impossible movements cannot be observed in naturalistic contexts.

The main results of our study were the comparable activation of premotor areas contingent upon observation of both possible and impossible hand movements and the stronger activation of PPC during observation of impossible than possible fingers movements.

Observational Representation of Moving Body Parts in Frontal Areas

The first main result showed that a set of frontal structures was selectively activated during observation of articulated body but not scissors movements, thus suggesting that the frontal neural system supposedly involved in action recognition can differentiate movements of body parts from movements of man-made non-biological objects. It is highly unlikely that such differences in activation were due to differences in stimulus parameters. We chose stimuli with comparable perceptual complexity and matched angular displacement and movement rate, which were by and large the two most important variables to control

Table 1

MNI coordinates of peaks of relative activation within regions activated by either finger or scissors movements, when comparing: (a) possible hand movements versus possible scissors movements [(possible hand movement - static hand) - (possible scissors movement - static scissors)]; and (b) impossible hand movements versus impossible scissors movements [(impossible hand movement - static hand) - (impossible scissors movement - static scissors)]

Anatomical description	MNI coordinates				Z-score
	Side	x	y	z	
(a) Possible hand movements versus possible scissors movements					
Inferior frontal gyrus (opercular)	L	-52	8	20	3.25
Postcentral gyrus (superior)	R	56	-24	48	4.30
Supramarginal gyrus	R	52	-36	40	3.85
Inferior parietal lobe	L	-40	-32	40	3.37
	R	56	-36	48	3.27
Middle temporal gyrus	L	-56	-48	0	4.04
	R	56	-56	4	3.81
Thalamus	L	-12	-20	0	3.01
(b) Impossible hand movements versus impossible scissors movements					
Inferior frontal gyrus (opercular)	R	56	12	28	2.61
Precentral gyrus (superior)	L	-28	-24	64	2.94
Precentral gyrus (inferior)	L	-60	4	24	3.60
Postcentral gyrus (superior)	L	-36	-36	64	3.00
	R	44	-36	64	3.48
Postcentral gyrus (inferior)	L	-64	-20	24	3.06
	R	64	-16	20	3.36
Supramarginal gyrus	L	-52	-40	28	3.35
	R	56	-36	36	4.76
Superior parietal lobe (anterior)	R	32	-44	56	3.93
Superior temporal gyrus	L	-56	-28	16	3.82
	R	52	-28	16	2.93
Middle temporal gyrus	L	-52	-60	8	3.83
	R	48	-56	8	3.33
Inferior temporal gyrus (posterior)	R	48	-60	-12	3.76
Middle occipital gyrus	L	-48	-80	8	2.57

Table shows local maxima >4 mm apart.

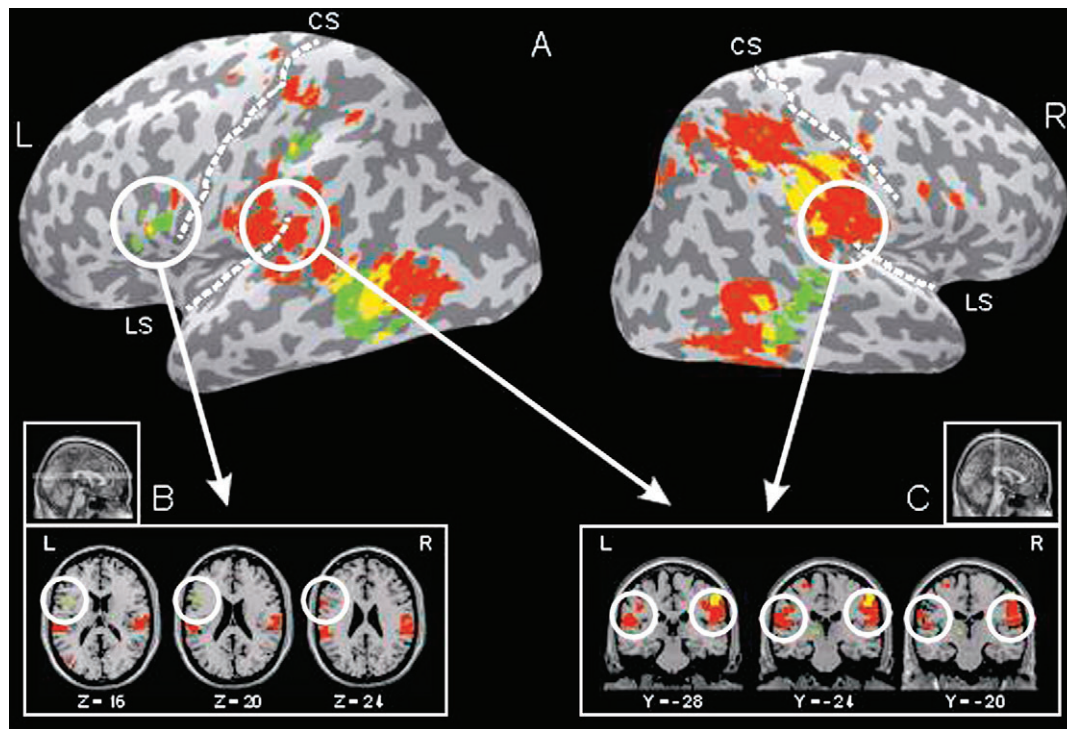


Figure 3. Regions of relatively higher activation during observation of possible finger versus possible scissors movements (green) and during observation of impossible finger versus impossible scissors movements (red). Yellow areas indicate regions of overlap. Group activation data are rendered on the reconstructed and unfolded cortical surface (A) and on selected transverse (B) and coronal (C) slices from a 'canonical' brain (Mazziotta *et al.*, 1995).

for. On the other hand, no differential activation of primary visual areas emerged when we compared the two types of stimuli. Moreover, our regions of interest should not be sensitive to low-level visual stimulus parameters (Schubotz and von Cramon, 2003). Similarly, it is unlikely that differences in eye movements made while viewing the different movies influenced the results. Indeed, we found no activation in areas classically considered to be involved in eye movement control, such as the frontal eye field or the intraparietal sulcus.

Our results are in keeping with a large number of neuroimaging and neurophysiological studies which demonstrate the involvement of premotor and motor cortices in action observation (Rizzolatti *et al.*, 1996a,b, 2001; Hari *et al.*, 1998; Iacoboni *et al.*, 1999; Buccino *et al.*, 2001, 2004a,b; Rossi *et al.*, 2002).

The central and somewhat surprising aspect of this result emerges in the comparisons of neural activity during possible and impossible actions. The comparable bilateral activation of premotor areas contingent upon action observation indicates that at least in these neural structures, humans represent actions independently of their actual execution. Thus, the premotor system does not take into account the biomechanical constraints the observed movements would involve if they were actually executed. This result seems to contrast the findings of other studies indicating that the premotor mirror system is active only during the observation of actions that are part of the observer's motor repertoire (Buccino *et al.*, 2004a).

One possible explanation of our result is that the similarity between the possible and impossible hand movements allowed our subjects to generalize implicit or even explicit simulation from one class of movements to the other. However, our results go beyond a strict account of the assumption that a direct

Table 2

MNI coordinates of peaks of relative activation in regions activated during observation of impossible versus possible hand movements

Anatomical description	MNI coordinates				
	Side	x	y	z	Z-score
Postcentral gyrus (inferior)	L	-64	-20	28	4.43
	R	60	-20	32	4.29
Supramarginal gyrus	L	-52	-24	32	3.59
	R	64	-28	40	4.77
Superior parietal lobe	R	32	-44	56	3.14
Superior temporal gyrus	L	-60	-28	16	2.70
Middle temporal gyrus	R	52	-68	4	2.89
Inferior temporal gyrus	R	48	-60	-12	4.18
Middle occipital gyrus	R	40	-88	4	3.54

Table shows local maxima more than 4 mm apart.

observation-execution simulation matching occurs in frontal areas.

Feeling Observed Movements in Parietal Areas

The second main result of the present study was that the PPC (Brodmann's areas 40 and 7) was significantly more active during the observation of impossible than possible hand movements. This activation was probably due to the crucial role played by the PPC in the sensorimotor transformations that link world-related and body-related sensations to action execution (Andersen *et al.*, 1997; Freund, 2003). Moreover, this activation suggests that PPC regions play a crucial role in determining whether the observed movement can actually be performed.

It has been suggested that the parietal areas may constitute the neural substrate for storage of kinesthetic limb postures and

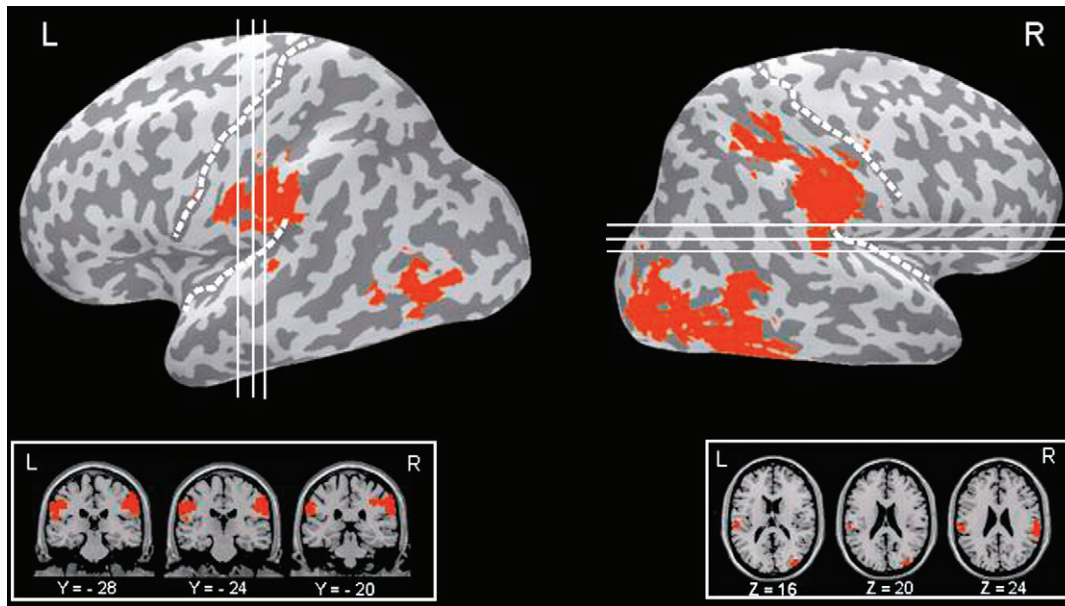


Figure 4. Regions of relatively higher activation during observation of impossible finger versus possible hand movements. Group activation data are rendered on the reconstructed and unfolded cortical surface and on selected coronal and transverse slices from a 'canonical' brain (Mazziotta *et al.*, 1995).

map these representations onto the premotor and motor regions containing the corresponding motor programs (Sirigu *et al.*, 1996). Thus, the activity of these networks may be fundamental for matching sensory input onto one's own body schema and thus coding the possibility of actually performing the same actions.

All of the experimental subjects reported that observation of impossible hand movements induced a variety of sensory feelings ranging from aversion to the sensation of joint stretch. In view of this, we postulate that the discrimination of visually observed impossible actions is not purely visual and that analysis of whether the movement of a body segment can actually take place automatically activates multimodal sensory networks.

The finding of a selective increase of the BOLD signal in the PPC during observation of impossible human actions may reflect the process of coding discrepancies between somatic mapping of visual input and action simulation carried out in frontal structures. The larger right than left PPC activation during observation of impossible hand movements is in keeping with this view and with previous neuroimaging studies showing selective right-sided parietal activation in conditions of conflict between visual and somatomotor signals (Fink *et al.*, 1999; Farrer *et al.*, 2003).

A significant increase of the BOLD signal in the left posterior thalamus was also found during observation of possible movements. Activation of the thalamus contralateral to a moving body part has been reported during motor execution (Binkofski *et al.*, 1999; Gerardin *et al.*, 2000; Farrer *et al.*, 2003; Agnew *et al.*, 2004). This is not surprising because motor execution is tightly linked to somatic feedback and because the thalamus, particularly its posterior part, is densely connected to the parietal cortex. Thalamic activation has also been found in neuroimaging studies of action observation (Stevens *et al.*, 2000; Manthey *et al.*, 2003). Although none of these studies provide any tentative explanation for the effect, we hypothesize

that the left-sided thalamic activation found in our study supports the general view that the neural structures activated during action observation largely overlap those activated during action execution.

Multisensory Mapping of Actions in the Extrastriate Body Area

Our fMRI study shows a temporo-occipital, predominantly right-sided activation during observation of biomechanically impossible biological actions. This activation is near/at EBA, a cortical area selectively activated by non-facial body stimuli (Downing *et al.*, 2001; Urgesi *et al.*, 2004). A recent fMRI study demonstrates that neural activity in EBA is modulated by actual or imagined movements of hands but not eyes (Astafiev *et al.*, 2004). The higher BOLD signal during observation of impossible movements, a condition in which onlookers report sensory feelings, not only suggests that EBA may be activated during action observation but also that this area codes body and action related stimuli multimodally. The temporo-occipital activation found in the present study can also be interpreted in a slightly different, by no means alternative, perspective. Previous PET studies show that temporal structures are involved in the perception of actions, with a right-sided predominance for meaningless actions (Grezes *et al.*, 1999; Decety *et al.*, 1997). Although a comparison of PET and fMRI data may not be straightforward, the greater activation of these multimodal areas for impossible than possible (or meaningless than meaningful) movements may have to do with the neural matching of visual and somatic information concerning observed and inner simulated actions.

In conclusion, our study indicates that different nodes of the fronto-parietal mirror system underlying action observation and execution deal with different aspects of the 'see-do' matching process. The frontal node codes a movement as biological while the parietal node discriminates impossible from possible human biological movements.

Notes

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