

SHORT COMMUNICATION

Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study

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Abstract

Functional magnetic resonance imaging (fMRI) was used to localize brain areas that were active during the observation of actions made by another individual. Object- and non-object-related actions made with different effectors (mouth, hand and foot) were presented. Observation of both object- and non-object-related actions determined a somatotopically organized activation of premotor cortex. The somatotopic pattern was similar to that of the classical motor cortex homunculus. During the observation of object-related actions, an activation, also somatotopically organized, was additionally found in the posterior parietal lobe. Thus, when individuals observe an action, an internal replica of that action is automatically generated in their premotor cortex. In the case of object-related actions, a further object-related analysis is performed in the parietal lobe, as if the subjects were indeed using those objects. These results bring the previous concept of an action observation/execution matching system (mirror system) into a broader perspective: this system is not restricted to the ventral premotor cortex, but involves several somatotopically organized motor circuits.

Introduction

In the monkey premotor cortex (area F5) there are neurons that discharge both when the monkey performs specific hand actions (e.g. grasping an object) and when it observes another individual performing the same or a similar action (Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996a). The hypothesis was forwarded that these neurons, called 'mirror neurons', subserve the capacity of individuals to recognise actions made by others.

There is growing evidence that a 'mirror' system, similar to that described in the monkey, also exists in humans. Electrophysiological studies (Hari *et al.*, 1998; Cochin *et al.*, 1999) showed that when a human subject observes hand actions there is a desynchronization of the motor cortex similar, although weaker, to that occurring during active movements. In agreement with these findings, transcranial magnetic stimulation (TMS) experiments showed that motor-evoked potentials recorded from hand muscles increase during the observation of hand movements (Fadiga *et al.*, 1995; Strafella & Paus 2000).

Because the motor cortex of primates does not receive a significant visual input, its activation, during observation of actions made by others, ought to be mediated by the premotor areas that are connected with it. This conclusion has been supported by brain imaging studies showing that during observation of hand/arm actions there is an activation of the ventral premotor cortex centred to the Broca's region (Grafton *et al.*, 1996; Rizzolatti *et al.*, 1996b; Decety *et al.*, 1997; Grezes *et al.*, 1998; Iacoboni *et al.*, 1999). Considering, however, that Broca's area is the cortical motor speech centre, the possibility cannot

be excluded that Broca's area activation, during action observation, were due to an internal verbalization of the observed actions rather than to a 'mirror' mechanism.

The main aim of the present study was to assess whether the observation of actions made with different effectors would activate specific parts of the premotor cortex in accord with the somatotopic motor organization of the region. This activation specificity, if proved, would show on one side, that the mirror system is not limited to hand action and on the other, would allow one to rule out the hypothesis that the activation of Broca's area, reported during hand action observation, was due to verbalization. If the verbalization hypothesis were true, Broca's area should be the major activation focus during action observation, regardless of the effector used.

The second aim was to determine to what extent the presence of an object influences the analysis of an observed action. When an individual acts on an object, a specific, pragmatic analysis of the object is carried out in the parietal lobe. This analysis is distinct from the semantic processing performed in the temporal lobe (Jeannerod, 1994; Milner & Goodale, 1995). Would the observation of object-related actions evoke this pragmatic analysis? An activation of pragmatic representations would be evidence, that during action observation, individuals internally 're-act' the observed action in terms of both action and the object acted upon.

Materials and methods

Subjects

Twelve healthy, right-handed subjects, aged 25–38 years-old took part in the experiment. All subjects (except two) were naive as to the purpose of the experiment. They all gave their written consent to the

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experimental procedure. The study was approved by the Ethical Committee of the Heinrich Heine University, Duesseldorf.

MRI scanner and scanning sequences

Functional magnetic resonance imaging (fMRI) measurements were performed on a 1.5 Tesla Siemens Vision scanning system using standard echo-planar imaging (EPI) and a standard radio frequency head coil for signal transmission and reception. Thirty consecutive slices orientated parallel to the anterior–posterior commissure plane and covering the whole brain were acquired. The following EPI sequences were used: repetition time, 5 s; signal-gathering time (echo-time), 66 ms; α , 90°; voxel size, 3×3×4 mm.

Experimental protocol

While being scanned, subjects were asked to carefully observe different videotaped object- and non-object-related actions, performed by another individual with different effectors (mouth, arm/hand and foot). These videotaped actions were presented on a screen, situated outside the scanner. Subjects could see them through a mirror (10×15 cm) which was positioned in the scanner in front of them. Videotaped actions were presented in sequences 25 s long. During each sequence the same action was presented 3–4 times. Each sequence was presented twice during the experimental session. The observed actions were: biting an apple and chewing (mouth actions); reaching and grasping a ball or a little cup with the hand and mimicking these actions without the object (hand actions) or kicking a ball or pushing a brake and mimicking these actions without the object (foot actions). Observation of both object- and non-object-related mouth, hand and foot actions (active condition) was contrasted with the observation of a static face, a static hand and a static foot, respectively, as a control condition. Static stimuli were presented for 25 s continuously. At the end of the experimental session, subjects had to report the actions they were presented with. All subjects reported them correctly.

Image analysis

Image analysis was performed on a SPARC II workstation (Sun Microsystems) using MATLAB (Mathworks Inc., Natick, MA, USA) and statistical parametric mapping package SPM97d (Friston *et al.*, 1995, 1997). Firstly, functional images of each condition were realigned to the tenth image to correct for head movements between scans. Then the images were coregistered and transformed into a standard stereotactic space, using the intercommissural line as the reference plane for transformation (Friston *et al.*, 1997). Active and control conditions were modelled using a delayed box-car reference vector, accounting for the delayed cerebral blood flow change after stimulus presentation. Significantly activated pixels were searched for by using the general linear model approach for time series proposed by Friston *et al.* (1995). Group activation maps were calculated by pooling the data for each condition across all subjects. Pixels were identified as significantly activated if they passed the highest threshold of Z-score (3.09) and belonged to a cluster of at least 10 activated pixels ($P < 0.05$, corrected for multiple comparisons). The activated pixels surviving this procedure were superimposed on high-resolution magnetic resonance (MR) scans of a standard brain (Montreal Neurological Institute, MNI). Clusters of activated foci were assigned to the regions of interest according to their centres of mass activity with the aid of Talairach coordinates (1988) and prominent sulcal landmarks. Furthermore, as far as Broca's region is concerned, Talairach coordinates were also compared with the coordinates of cytoarchitectonically defined probability maps (Amunts *et al.*, 1999)

Results

The results of the experiment are shown in Figs 1–3. Frontal and parietal activations related to action observation are presented in colour. Other activations (mostly occipital) are shown in grey. These latter activations (probably due to stronger activation of visual areas with moving stimuli) will not be discussed here.

Activations during mouth action observation are shown in Fig. 1. During the observation of non-object-related mouth actions (chewing, a), activation foci were present in areas 6 and 44 on both sides and in area 45 in the right hemisphere. Right hemisphere activation was larger and stronger than left hemisphere activation. During the observation of object-related mouth actions (biting an apple, b), the pattern of premotor activation was similar, although weaker, to that found during non-object-related actions. In addition, two activation foci were present in the parietal lobe. These foci were larger in the left than in the right hemisphere. The rostral focus was located in area 40 (area PF of von Economo, 1929), the caudal focus in area 39 (area PG).

Figure 2 shows activation foci relative to observation of arm/hand actions. During the observation of non-object-related hand actions (mimicking reaching to grasp, a) there was a bilateral activation of area 6 that was located dorsal to that found during mouth movement observation. During the observation of object-related arm/hand actions (reaching-to-grasp movements, b) there was a bilateral activation of premotor cortex plus an activation site in area 44. Most interestingly, as in the case of the observation of mouth movements, two activation foci were present in the parietal lobe. The rostral one was located inside the intraparietal sulcus, in an area caudal and dorsal to that found in the mouth movement observation condition. This area probably corresponds to the anterior intraparietal area of the monkey. The caudal focus was in area 39 (area PG). This last focus considerably overlapped that found during mouth movement observation.

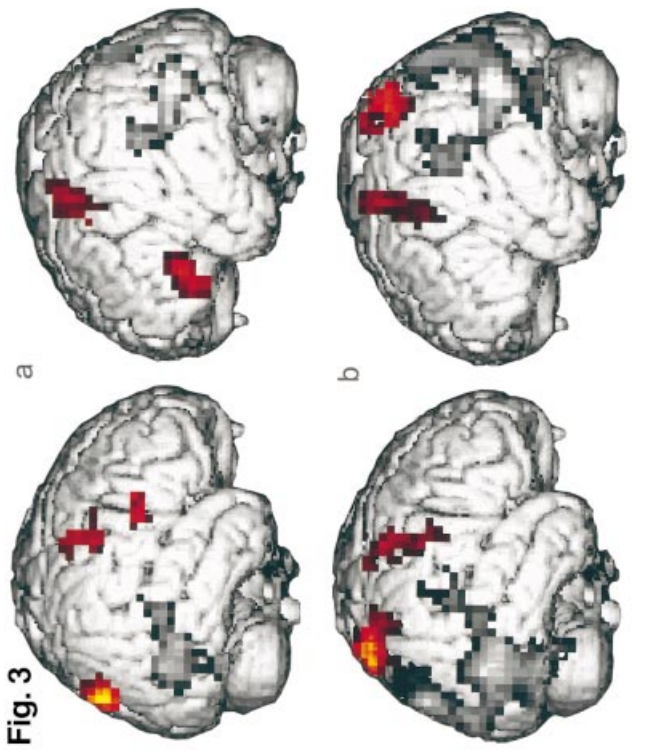
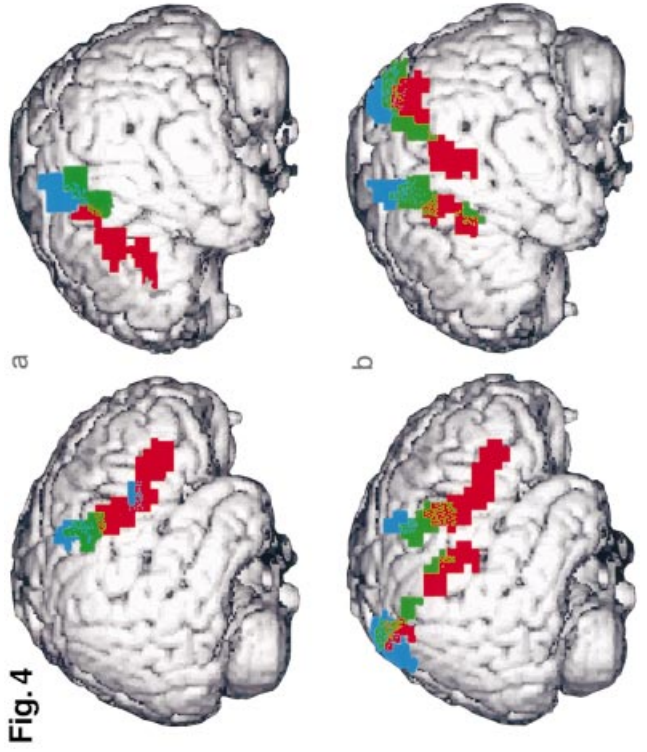
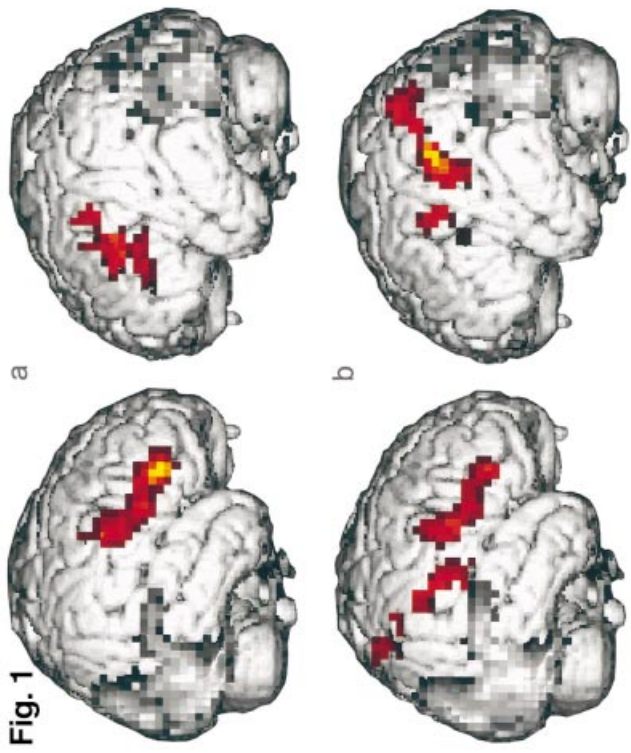
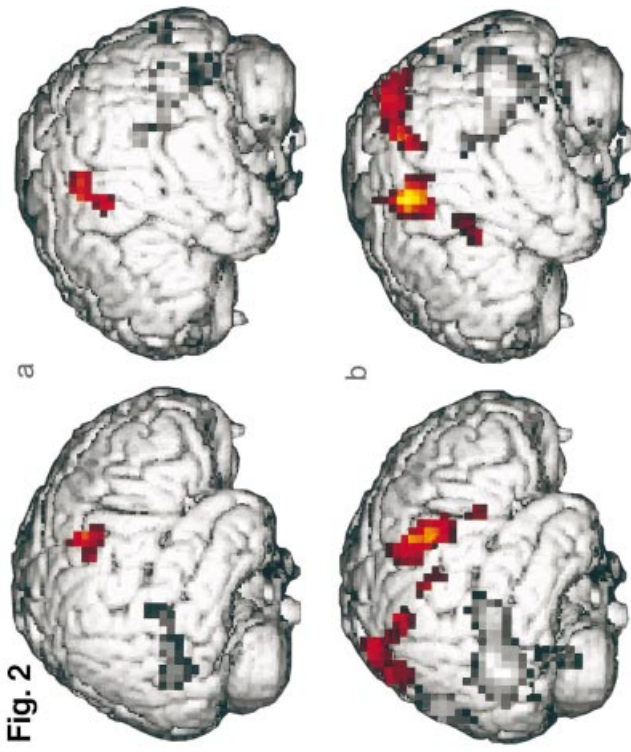
Figure 3 shows activation foci elicited by observation of foot actions. During the observation of non-object-related foot actions (mimicking ball kicking or brake pushing, d), there was an activation of a dorsal sector of area 6. There also was an activation of the frontal lobe (rostrally located). Because we have no explanation for this activation (found only in this condition), we will not comment on it further. During the observation of object-related foot actions (kicking a ball or pushing a brake, b), there was, as in the previous condition, an activation of a dorsal sector of area 6. In addition, there was an activation of the posterior part of the parietal lobe. The parietal activation was in part located in Brodmann's area 7 [(PE)], in part it overlapped the activation seen during mouth and hand actions (Brodmann's area 39/PG).

Figure 4 gives a global picture of the activations found during observation of mouth, hand and foot actions. It is evident that both the premotor cortex and the parietal lobe activation foci are somatotopically organized. The premotor somatotopy follows a pattern similar to that of the classical motor homunculus (Penfield & Rasmussen, 1952). In the parietal lobe, the mouth is represented rostrally while the foot is located caudally.

Table 1 shows the Talairach coordinates and Z scores of the activated foci during the observation of object- and non-object-related mouth, hand, and foot actions.

Discussion

The results of the present experiment show that when an individual observes actions (made by another individual) performed with different effectors, different sectors of the premotor cortex are



activated. During mouth actions, there is a bilateral activation of ventral area 6 and area 44 plus an activation of the right area 45. During hand actions, a more dorsal part of ventral area 6 plus a dorsal sector of area 44 are recruited in both hemispheres. Finally, the observation of foot actions elicits an activation of a dorsal sector of area 6, bilaterally. There is, therefore, a clear topographic shift in the premotor cortex activation from ventral to dorsal when the effector used in the observed action moves from mouth to arm/hand and to foot, respectively. This shift is congruent with the classical motor organization of the region (see Penfield & Rasmussen, 1952).

These results are important for two reasons. First, the effector related somatotopic activation pattern in the premotor cortex during

the mere observation of actions proves that, in humans, the mirror system is not restricted to hand actions, but includes a rich repertoire of body actions. It therefore constitutes the neural substrate for a matching mechanism mapping the observed actions on the observer's motor representations. Second, these results definitively rule out the interpretation that cortical activation during action observation is due to verbalization.

A further important result of the present experiment is the demonstration of a marked difference between the activation during the observation of object-related and non-object-related actions. Any time an object is the target of an action, the parietal lobe is strongly activated. This object-related activation is also somatotopically

TABLE 1. Talairach coordinates and Z-scores of the activated foci during observation of object- and non-object-related mouth, hand, and foot actions

Actions/Brain area	Activated foci during the observation of								
	Object-related actions				Non-object-related actions				
	x	y	z	Z-score	x	y	z	Z-score	
Mouth actions									
Brodmann's area 6									
R	48	0	32	4.38	52	0	32	3.28	
L	-56	0	36	4.18	-52	4	44	3.55	
Brodmann's area 44									
R	60	8	24	3.76	56	12	16	3.79	
L	-64	12	20	3.01	-60	16	16	3.07	
Brodmann's area 45									
R	60	16	20	4.13	60	28	20	4.31	
Inferior parietal lobule									
R	52	-24	20	3.31					
	52	-32	44	3.39					
L	-36	-52	56	5.16					
	-60	-24	36	4.21					
Arm/hand actions									
Brodmann's area 6									
R	48	0	44	4.66	52	0	48	3.64	
L	-56	-4	44	5.84	-60	-4	40	3.72	
Brodmann's area 44									
R	56	12	12	3.01					
L	-64	4	24	3.72					
Anterior intraparietal area									
R	40	-40	52	4.55					
L	-36	-40	52	4.63					
Foot actions									
Brodmann's area 6									
R	40	-4	60	3.38	44	-4	56	3.93	
L	-32	-8	64	3.30	-40	-4	60	4.05	
Superior parietal lobule									
R	24	-60	68	5.69					
L	-32	-64	60	5.05					

R, right hemisphere; L, left hemisphere; x, y, z, Talairach coordinates.

FIG. 1. Observation of mouth actions. Projections of the activation foci on the lateral surface of a standard brain [Montreal Neurological Institute (MNI)] during the observation of non-object-related (chewing: a) and object-related (biting an apple: b) mouth actions.

FIG. 2. Observation of hand actions. Projections of the activation foci on the lateral surface of a standard brain (MNI) during the observation of non-object-related (mimicking grasping of a cup or a ball, without object: a) and object-related (grasping a cup or a ball: b) hand actions.

FIG. 3. Observation of foot actions. Projections of the activation foci on the lateral surface of a standard brain (MNI) during the observation of non-object-related (mimicking kicking a ball or pushing a brake, without the object: a) and during the observation of object-related foot actions (kicking a ball or pushing a brake: b) foot actions.

FIG. 4. Somatotopy of premotor and parietal cortices as revealed by action observation. (a) Observation of non-object-related actions. (b) Observation of object-related actions. Activation foci, shown in detail in the three previous figures, are projected on the lateral surface of a standard brain (MNI). Red, activation during the observation of mouth movements; green, activation during the observation of hand movements; blue, activation during the observation of foot movements. Overlap of colours indicates activation foci present during observation of actions made by different effectors.

organized and depends on the effector used. During the observation of mouth actions, there is an activation of the rostral part of the inferior parietal lobule (area 40). During the observation of hand actions, a more posterior sector of area 40, inside the intraparietal sulcus, becomes active. This sector closely corresponds to that shown to be active during object manipulation (Binkofski *et al.*, 1999). It has been suggested that this sector is the human homologue of monkey anterior intraparietal area. The observation of foot actions activates predominantly the posterior part of the superior parietal lobule. Finally, in all conditions there is activation of area 39 (area PG).

Although the motor organization of the parietal lobe is not fully established, an organization similar to that here described for action observation in humans can be recognized for active movements in nonhuman primates. In the monkey, mouth movements are represented in the rostral part of PF (Leinonen & Nyman, 1979; Fogassi *et al.*, 1998), distal hand movements in the anterior intraparietal area (Sakata *et al.*, 1995) and arm reaching movements, posteriorly on the medial bank of the intraparietal sulcus (Colby & Duhamel, 1991; Snyder *et al.*, 1997). Furthermore, clinical and brain imaging studies strongly suggest that a segregated pattern of effector representations in the parietal lobe is also present in humans (De Renzi, 1982; Jeannerod, 1986; Pause *et al.*, 1989; Seitz *et al.*, 1991).

It is generally accepted that a fundamental role of the parietal lobe is to describe objects for action (Jeannerod, 1994; Jeannerod *et al.*, 1995; Milner & Goodale, 1995). This 'pragmatic', action-orientated object description has been contrasted with the 'semantic' description coded in the infero-temporal lobe (Milner & Goodale, 1995; Jeannerod *et al.*, 1995). The results of the present experiment indicate that a 'pragmatic' analysis is also carried out when an individual observes an object-directed action made by another individual. If action understanding were based on higher cognitive functions, this parietal analysis would be unnecessary.

Taken together, the results of the present experiment strongly support the view that during action observation there is a recruitment of the same neural structures which would be normally involved in the actual execution of the observed action. When individuals observe an action, they code that action in terms of the related voluntary movements. The 'seen' actions are mapped onto the corresponding motor representations of the frontal lobe and, in the case of object-related actions, the 'seen' objects on the effector-related, pragmatic representations, in the parietal lobe.

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Abbreviations

EPI, echo planar imaging; fMRI, functional magnetic resonance imaging; MNI, Montreal Neurological Institute; TE, signal- (echo-) gathering time; TR, sequence repetition time.

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