RAPID COMMUNICATION

A PET Exploration of the Neural Mechanisms Involved in Reciprocal Imitation

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Imitation is a natural mechanism involving perception–action coupling which plays a central role in the development of understanding that other people, like the self, are mental agents. PET was used to examine the hemodynamic changes occurring in a reciprocal imitation paradigm. Eighteen subjects (a) imitated the actions of the experimenter, (b) had their actions imitated by the experimenter, (c) freely produced actions, or (d) freely produced actions while watching different actions made by the experimenter. In a baseline condition, subjects simply watched the experimenter's actions. Specific increases were detected in the left STS and in the inferior parietal cortex in conditions involving imitation. The left inferior parietal is specifically involved in producing imitation, whereas the right homologous region is more activated when one's own actions are imitated by another person. This pattern of results suggests that these regions play a specific role in distinguishing internally produced actions from those generated by others. © 2002 Elsevier Science

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INTRODUCTION

Motor imitation involves observing the action of another individual and matching one's own movements to those body transformations. Imitation has recently become the focus of interest from various disciplines. Although developmental psychologists have long been concerned with imitation, the field has burgeoned with the finding that newborns imitate facial gestures, suggesting an innate system for coupling the perception and production of human acts (Meltzoff and Moore, 1977, 1997). Research on neonatal imitation has not only emphasized its critical role in nonverbal communication but has also suggested that it provides an innate link between mental states and actions (Gopnik and Meltzoff, 1997). Imitation might serve, through development, as an automatic way of interpreting the behaviors of others in terms of their underlying intentions and desires (Meltzoff, 1995; Nadel and Butterworth, 1999). The development of new techniques has allowed evolutionary psychologists to study imitation across species (Byrne, 1999). Imitation is also attracting increasing attention of computer scientists and engineers seeking to design robots that will act more like humans (Schaal, 1999).

Many cognitive and developmental psychologists postulate a common coding for actions performed by the self and by another person (Barresi and Moore, 1996; Gopnik, 1993; Meltzoff and Moore, 1995; Prinz, 1997). In recent years, neurophysiological evidence, ranging from electrophysiological recordings in monkeys to neuroimaging in humans, suggests that this shared representation of action is subserved by specific cortical regions (for a meta-analysis of the neuroimaging studies in humans, see Grèzes and Decety, 2001). For example, producing an action, observing another individual performing it, and even mentally simulating it involve a common set of regions in frontal and posterior parietal lobes (Decety et al., 1994, 1997; Fadiga et al., 1995; Rizzolatti et al., 1996; Hari et al., 1998; Grèzes et al., 1998, 1999; Decety and Grèzes, 1999; Decety, 2001). There is thus convergence from both brain and behavioral sciences on the idea that the same representations are used for both reading others' actions and producing them. However, this raises a new issue: we easily distinguish the actions we produce from those generated by others. How are actions represented in the brain such that similarities between self and other are perceived, but confusion between self and other does not occur (Blakemore et al., 1998b), except in the case of certain neurological and psychiatric pathologies. We believe that imitation paradigm focusing on mutual relations is suited to tackle this question of intersubjectivity since the visual and the
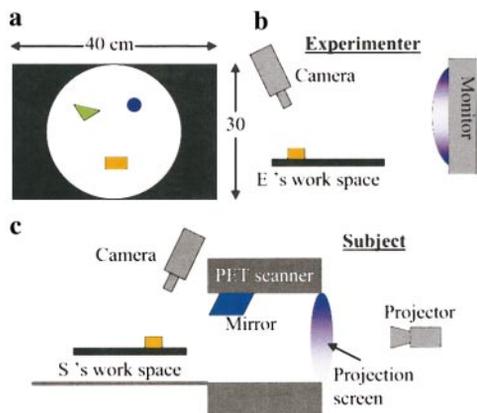
FIG. 1. Experimental set-up. (a) Both workspaces consisted in a board (black surface of 33 × 40 cm with white 30-cm-diameter circle in the center) on which three easily graspable objects of different shapes (cylindrical, cubic, and triangular) and colors (green, purple, and orange) were placed. (b and c) One meter above the experimenter's (b) and the subject's (PET scanner with NEC projector; (c) workspaces, a video camera was positioned at an angle of 88°. A video device located behind the PET scanner was used to project the visual feedback to the subject, either the experimenter's hand actions in conditions A, B, D, and E or the subject's hand actions in C.

motor components are similar when one imitates or is imitated so that the key distinction is the individual controlling the action, either the self or the other.

Despite the importance and the value of imitation, few studies using neuroimaging techniques have explored its neural substrate in the healthy brain. Recently a fMRI study reported activation of Broca's area and parietal cortex during reproduction of finger movements (Iacoboni *et al.,* 1999). Here, we used positron emission tomography (PET) to examine the hemodynamic changes produced when subjects were imitating the experimenter's actions and in the reverse case, when the subjects' actions were imitated by the experimenter. We also used control conditions in which subjects saw their own manual actions with objects and were presented with other tasks to control for activation related to movement production not specific to the imitation task. In all cases the same specially constructed device was used to present the stimuli to the subjects in the PET apparatus (Fig. 1). To our knowledge, it is the first neuroimaging study using such a sharp definition of imitation, i.e., the novelty of each trial and the similarity of the goal and of the means to achieve it (Byrne and Russon, 1998), as well as the first time
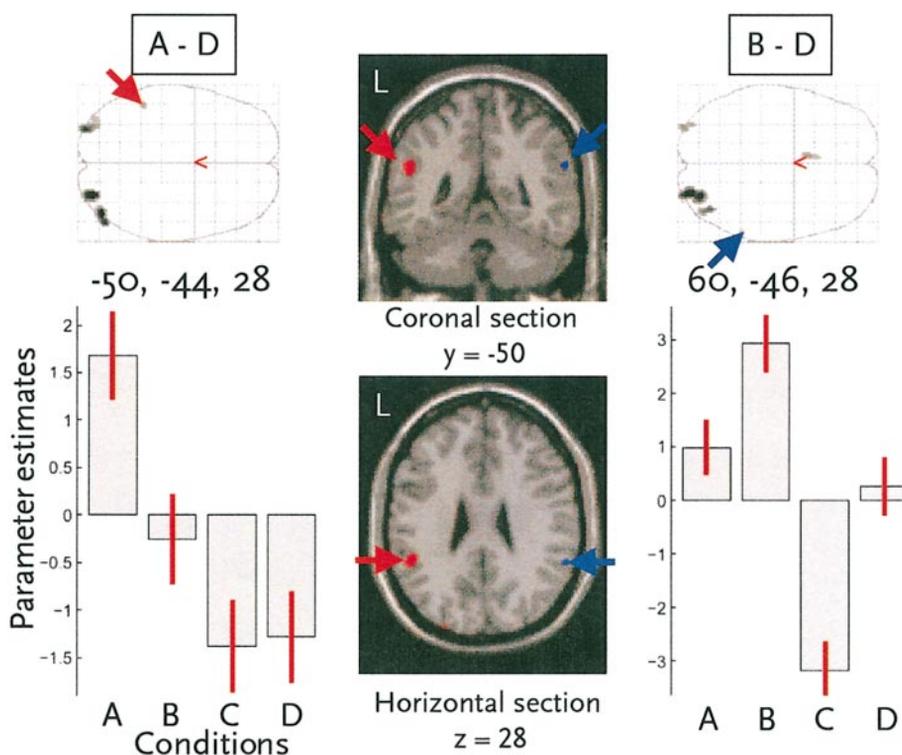

FIG. 2. Inferior parietal lobule activity. At the center, the active cluster in the IPL from the A–D (red) and B–D (blue) contrasts are superimposed to coronal and horizontal sections of a standard brain (L, left hemisphere). Glass views of the activation foci in the A–D and B–D contrasts are shown respectively on the left and on the right. Graphs show parameter estimates (red bars, standard deviation) at the MNI coordinates indicated above, corresponding to the IPL clusters indicated by arrows in the glass rendering, respectively left IPL, indicated by the red arrow on the left, and right IPL, indicated by the blue arrow on the right.
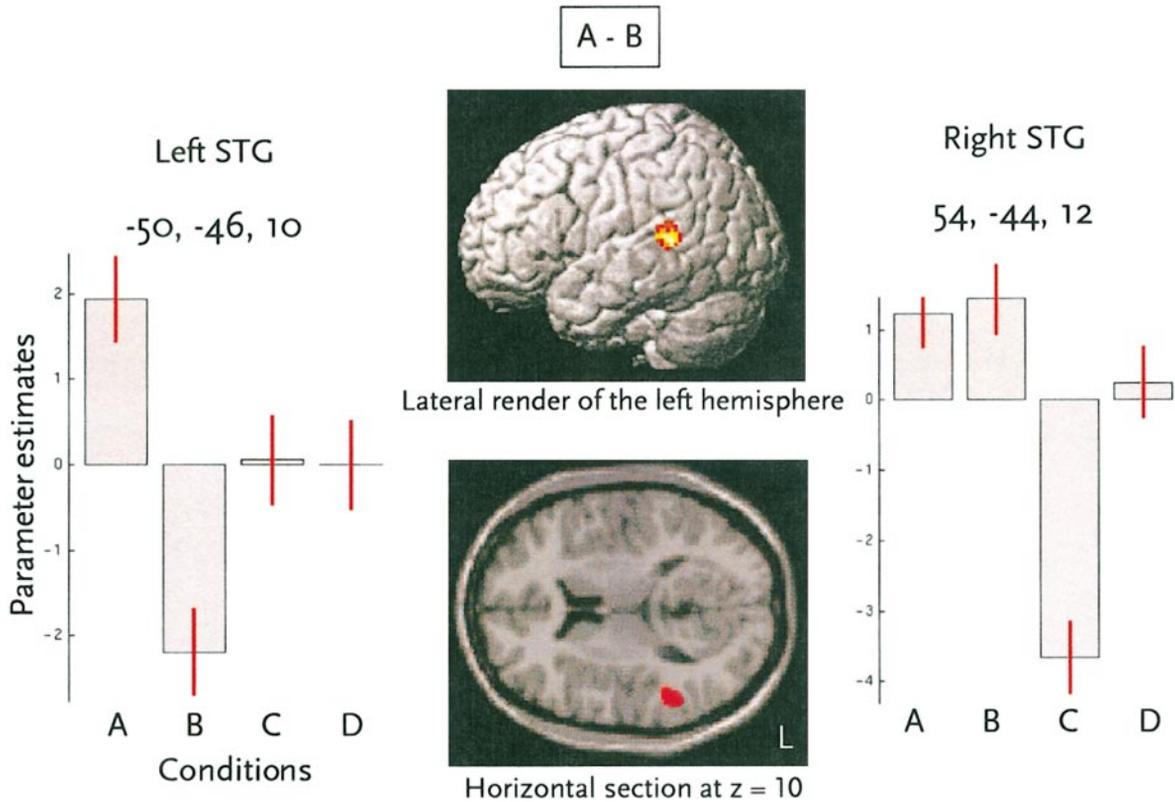
FIG. 3. Posterior superior temporal gyrus activity. At the center, the active cluster in the STG from the A–B contrast is superimposed to a left lateral rendering and a horizontal section of a standard brain (L, left hemisphere). Graphs show parameter estimates (red bars, standard deviation) at the MNI coordinates indicated above, corresponding respectively to the left and right regions on the left and right.

tests were devised to assess brain correlates of imitating versus being imitated by another person.

It was predicted that both imitation conditions would activate a common set of cortical areas, which reflects the mapping between the self and the other, i.e., shared motor representations that are known to recruit premotor and parietal regions (Jeannerod, 1999). In addition, we expected that some specific regions or modulation of the activity in the regions subserving shared motor representations would differentiate imitating from being imitated. Furthermore, based on patient studies as well as neuroimaging studies of normal subjects, we hypothesized differential involvement of the inferior parietal lobule. Lesions of this region in the left hemisphere may lead to apraxia, which is often associated with imitation or pantomime impairments, whereas similar lesions in the right hemisphere are often associated with unilateral neglect or body awareness disorders. Recently, Ruby and Decety (2001) reported left parietal activation when subjects mentally simulated an action with a first-person perspective and right parietal activation when subjects simulated an action with a third person perspective, i.e., imagining the action of the other. In the proposed experiment, we therefore expect to find the left parietal cortex to be associated with imitation of the other by the self (producing imitation) and the right parietal cortex to be associated with imitation of the self by the other (having one's actions imitated).

MATERIAL AND METHODS

Subjects

Eighteen healthy right-handed male volunteers (ages 25 ± 3 years) gave informed consent in this study, which was approved by the local Ethics Committee (Center Léon-Bérard, Lyon). They were paid for their participation.

Experimental Set-up

The experimental set-up consisted in a work space with three objects, as illustrated in Fig. 1, and a camera connected to a video system that allowed online distribution of the video signal to channels (video recorder, monitor, and NEC projector). Cameras recorded the subject's and the experimenter's work spaces with the same orientation toward the hands and with the same angle, so that both signals could be superimposed on the experimenter's video monitor. A

mirror was placed in front of the subject's head in the PET scanner so that he could see the reflection of the screen from the video projector. The distance from the subject's eyes to the screen was about 75 cm. All the visual events were visible to the subject on the mirror.

Activation Conditions

Each action consisted of right-hand manipulations of one of the three objects in order to build small 3-D configurations. In all conditions except the baseline, subjects performed such actions, and, depending on the conditions, they were shown either the experimenter manipulation or their own manipulation of the same objects. To minimize the delay between subjects' and experimenter's actions in the imitation conditions (A and B), both were required to produce imitation of hand actions "online." Subjects and experimenter underwent extensive training in the PET environment 1 day before the scanning session in order to be familiarized with the experimental set-up and to minimize the delay between the actions performed by the subjects and those seen. This training lasted until this latter aspect was satisfactorily met. All actions with objects were performed at a rather slow pace (around 2 s for an object's move) to ensure matching of the manipulation rate between the experimenter and the subjects.

The conditions of interest, A and B, correspond to the two situations of reciprocal imitation. In both, subjects observed the experimenter's actions matching the ones they performed. Two stimulus characteristics must be carefully controlled to make sense of A and B, namely observing matching manipulations and seeing the experimenter's hand. We therefore designed two control conditions, C and D, to address these issues. In C, subjects observed a direct feedback from their own matching manipulation projected on the mirror, and in D, they observed nonmatching object manipulations performed by the experimenter. The last condition, E, was a baseline controlling manipulation-related activity.

- In condition A (Imitation of the other by the self), subjects were shown the experimenter's hand manipulating the objects and were instructed to imitate his actions.
- In condition B (Imitation of the self by the other), subjects were instructed to manipulate the objects at will and were shown the experimenter imitating their actions.
- In condition C (Control: self action), subjects were instructed to manipulate the objects at will and were shown their own actions.
- In condition D (Control: different action), subjects were instructed to manipulate the objects at will and were shown the experimenter performing different manipulations with the same objects.
- In condition E (Control: observing other's action), subjects were instructed to stay still and watch the experimenter manipulating the objects.

The order of the conditions was randomized and counterbalanced within and between subjects. Prior to each PET session, subjects were fully informed about the forthcoming condition. In particular they knew in advance whether they were going to imitate the experimenter (A) or to be imitated by the experimenter (B) in the two reciprocal imitation conditions. There were no ambiguities in the stimuli shown in each condition, either the experimenter's or their own hand acting. None of the subjects reported confusion between conditions.

PET Acquisition

A Siemens CTI HR+ (63 slices, 15.2-cm axial field of view) PET tomograph with collimating septa retracted operating in 3-D mode was used. Sixty-three transaxial images with a slice thickness of 2.42 mm without gap in between were acquired simultaneously. A venous catheter to administer the tracer was inserted in an antecubital fossa vein in the left forearm. Correction for attenuation was made using a transmission scan collected at the beginning of each study. After a 9-mCi bolus injection of $H_2^{15}O$, scanning was started when the brain radioactive count rate reached a threshold value and continued for 60 s. Integrated radioactivity accumulated in 60 s of scanning was used as an index of rCBF. The interval between successive scans was 8 min. Ten scans were acquired per subject, representing two replications of the five activation conditions.

Statistical Analysis

Functional image analysis was performed with statistical parametric mapping software (SPM99; Welcome Department of Cognitive Neurology, UK, see Friston *et al.,* 1995) implemented in Matlab 5.3 (Math Works, Natick, MA). The scans of each subjects were automatically realigned and then stereotactically normalized into the space of the MNI template used in SPM99. Images were then smoothed with a Gaussian kernel of 12-mm full-width at half-maximum. The voxel dimensions of each reconstructed scan were $2 \times 2 \times 4$ mm in the *x, y,* and *z* dimension, respectively. Global differences in cerebral blood flow were covaried out for all voxels, and comparisons across conditions were made using *t* statistics, SPM{*t*}. The SPM{*t*} were transformed into a *Z* distribution (SPM{*Z*}) and thresholded at $P < 0.0001$ uncorrected for multiple comparisons since the analysis was hypothesis driven. Subsequent analysis of the activation clusters of interest were performed using condition-specific parameter estimates, which reflect the adjusted rCBF relative to the fitted mean and expressed as a percentage of whole-brain mean blood flow in the most activated voxel of the cluster of interest.

TABLE 1

Areas of Increased rCBF in the Contrasts between Imitation of the Other by the Self and Self Action (A–C) and Imitation of the Self by the Other and Self Action (B–C)

Region	x, y, z	Z values A–C	Z values B–C
R supramarginal gyrus	54, −52, 40	6.61	8.08
R medial frontal gyrus	14, 30, 40	4.72	4.68
Medial frontal gyrus	0, 44, 38	6.18	4.04
R middle frontal gyrus	46, 20, 30	4.20	6.21
R superior frontal gyrus	20, 54, 20	4.62	—
R caudate nucleus	14, 12, 10	—	4.45
R inferior frontal gyrus	52, 22, 8	4.90	4.42
L pre-SMA	−6, 12, 56	—	3.91
L posterior cingulate	−12, −50, 40	—	4.29
L supramarginal gyrus	−54, −48, 24	5.77	—

Note. All *Z* values noted are *P* < 0.0001; voxel extent threshold, 10. R, right hemisphere; L, Left hemisphere. Coordinates correspond to the MNI atlas.

RESULTS

The main effect of right-hand manipulation of objects, calculated by contrasting each of the first three conditions (A to C), in which the subjects manipulate objects, to the last one (D), revealed a similar activation pattern in the left primary sensorimotor cortex, contralateral to the hand used by the subjects, and in the bilateral ventral premotor, superior parietal, and cerebellar areas. This is unsurprising, since these areas are known to be involved in hand action control (Passingham, 1993).

The two conditions involving imitation, i.e., Imitation of the other by the self (A) and Imitation of the self by the other (B), were compared to the two control conditions, Self action (C) and Different action (D). The results for the former comparison are given in Table 1 and the results for the latter are in Table 2.

The contrasts shown in Table 1 revealed common activated foci in the right inferior parietal lobule, centered on the supramarginal gyrus and extending to the posterior part of the superior temporal gyrus, in the medial frontal gyrus, and in the right middle and inferior frontal gyri. There was an increase of the *Z* value of the cluster in the right inferior parietal lobule, activity from the (B–C) contrast being superior to that from the (A–C) contrast. Specific rCBF increase was found in the left supramarginal gyrus for the first contrast (A–C) and in the posterior cingulate and the pre-supplementary motor area (pre-SMA) in the left hemisphere for the latter contrast (B–C).

The contrast with Different action (D) yielded common activation foci bilaterally in the occipital region. Specific rCBF increases were found in the left supramarginal gyrus for the A–D contrast and in the supra-

TABLE 2

Areas of Increased rCBF in the Contrasts between Imitation of the Other by the Self and Different Actions (A–D) and Imitation of the Self by the Other and Different Actions (B–D)

Region	x, y, z	Z values A–D	Z values B–D
R intraparietal sulcus	28, −82, 40	—	4.63
R supramarginal gyrus	60, −46, 28	—	3.73
R middle occipital gyrus	26, −88, 18	4.92	5.60
R inferior occipital gyrus	44, −80, −2	5.53	4.15
L Pre-SMA	−6, 12, 68	—	3.48
L supramarginal gyrus	−50, −44, 28	4.25	—
L middle occipital gyrus	−28, −94, 4	5.09	3.80

Note. All *Z* values noted are *P* < 0.0005; voxel extent threshold, 10.

marginal gyrus and posterior intraparietal sulcus in the right hemisphere as well as in the left pre-SMA for the B–D contrast.

The bilateral pattern of activity in the supramarginal gyrus bilaterally was further investigated using parameter estimates in the parietal clusters defined in Table 2 (Fig. 2).

The two conditions involving imitation provide an interesting comparison with one another: in both cases the produced and observed actions have a matching relation, but in one the subject is intentionally choosing the action and in the other the subject is imitating the action he is shown. Their direct comparison is given in Table 3.

TABLE 3

Areas of Increased rCBF in the Contrast between Imitation of the Other by the Self and Imitation of the Self by the Other (A–B) and in the Reverse Contrast (B–A)

Region	x, y, z	Z values
A–B		
R inferior lingual gyrus	20, −44, 10	3.58
L inferior frontal gyrus	−34, 12, 32	3.89
L middle occipital gyrus	−48, −72, 20	3.47
L superior temporal gyrus	−50, −42, 10	4.99
L superior anterior temporal gyrus	−42, −20, 0	3.76
B–A		
R medial frontal gyrus	20, 24, 40	3.95
R supramarginal gyrus	56, −46, 28	2.93*
R middle frontal gyrus	28, 40, 18	3.66
R inferior temporal gyrus	66, −52, −12	3.82
L pre-SMA	−4, 12, 66	3.97
L posterior cingulate	−12, −70, 44	3.54
L medial frontal gyrus	−12, 20, 38	4.14
L anterior cingulate	−4, 28, 20	3.51
L orbital gyrus	−18, −52, 20	3.79

Note. All *Z* values noted are *P* < 0.0005 (except *P* < 0.002); voxel extent threshold, 10.

DISCUSSION

The dual aims of this study were to explore the cerebral correlates of imitation and to identify brain mechanisms involved in agency by contrasting two types of imitative relations, producing imitation and being imitated. Our results show that in addition to the network involved in motor control (primary sensorimotor, ventral premotor, superior parietal, and cerebellum), there is a massive overlap between regions of rCBF increase (the inferior parietal lobe and the frontal cortex) in the two tasks with imitation compared to the Self action control (Table 1). The same is true for the common activated clusters in the occipital cortex comparing the imitation conditions and the Different action control (Table 2).

Two competing hypotheses might be proposed to explain these overlaps, either the involvement of these common regions in the two tasks of interest or a relative decrease of activity in the control conditions. Because condition D clearly involves a conflict between vision and action, occipital activity found in contrasts A–D and B–D could be related to a relative decrease of the visual cortex activity by the task requirements in condition D or to an attentional top–down effect in conditions A and B (Büchel et al., 1998). These hypotheses are not mutually exclusive. Conversely, condition C consists of simply acting on objects with visual feedback and is less cognitively demanding than A and B. It is therefore unlikely that task requirements cause a relative decrease of activity in the common areas described in A–C and B–C. These parietal and frontal clusters are better explained by similar cognitive processing involved in both conditions A and B, among which is the observation of actions performed by another person.

The frontal and right inferior parietal activated foci found in both A–C and B–C could also be explained by the absence of visual feedback in control of action. This issue was investigated by Fink et al. (1999), who reported increased neural activity in the posterior parietal cortex and dorsolateral prefrontal cortex bilaterally during bimanual coordination tasks when there is a mismatch between expected and realized sensorimotor states. No frontal activity was detected when contrasting the two conditions of interest to D, in which visual feedback of the subjects' action was also absent. These results therefore corroborate the interpretation that the right frontal activity is related to the absence of visual feedback.

Activation in the pre-SMA seems to be related to its involvement in action control. The pre-SMA is found in all contrasts related to imitation of the self by the other (B–C, B–D, B–A; see tables). This confirms, at first glance, the involvement of pre-SMA in self-produced actions (Passingham, 1993) since the subjects freely select their actions in condition B. However, the activation of the pre-SMA when contrasting condition B to C and D is an intriguing finding since actions are also internally selected in conditions C and D. The pre-SMA has been found to be activated by the mere observation of actions performed by other (see a meta-analysis by Grèzes and Decety, 2000), and only in condition B do subjects freely act and see matching actions performed by another person. Therefore, a possible explanation to account for this pattern of activity is that two components influence the activity in this area: selection of the action and observation of a matching action performed by others.

Medial prefrontal areas are found to be activated in contrasts between both imitation conditions and Self action (Table 1). This region has been reported in monitoring the sensory consequences of self-produced versus externally produced events (Blakemore et al., 1998a). Moreover medial prefrontal and paracingulate areas are known to be critically involved in theory of mind or mentalizing activities as shown by a number of neuroimaging studies (reviewed by Frith and Frith, 1999; Shallice, 2001). Interestingly the activation of the posterior cingulate cortex is found only when subjects are imitated by the other. The involvement of the medial prefrontal cortex may come into play as a function of intersubjectivity process that is implied in imitation. To imitate is to take the other's perspective, whereas to be imitated is the reverse. In general, the findings of a strong involvement of the medial prefrontal cortex in the current study fits with the link between imitation and mentalizing that has been proposed by psychologists based on behavioral–developmental data and theorizing (e.g., Meltzoff, 1999; Meltzoff and Brooks, 2001; Nadel and Butterworth, 1999).

The superior temporal region is known to be activated by observation of socially meaningful hand gestures, suggesting that it is sensitive to stimuli that signal the actions of another individual (Hietanen and Perrett, 1993; Allison et al., 2000). In a recent review, Frith and Frith (1999) emphasized the role of the superior temporal gyrus (STG) in the ability to distinguish between actions of the self and of other. Not only was the posterior part of the right STG found activated in both contrasts between conditions containing imitation (A and B) and Self action, but importantly, it was more activated in the left hemisphere when subjects imitated the other (A–B; Fig. 3).

This difference in the hemispheric lateralization in the STG is an intriguing finding. It may be a neural basis of the distinction between first- and third-person information conveyed through visual modality. Based on our results, one may suggest the hypothesis that right STG is involved in the genuine visual analysis of the other's actions, while the left region is concerned with the analysis of the other's actions in relation to the self's motor intention. Also compatible with this idea are the findings that bilateral increases in the

posterior STG region have been detected when subjects observe actions for deferred imitation (Grèzes *et al.,* 1998). Of course, further research is needed to assess this hypothesis. This result may provide neurophysiological grounds for the cognitive-developmental model proposed by Barresi and Moore (1996), Gopnik and Meltzoff (1997), and others in which the monitoring of both first-person information (i.e., self-generated signals) and third-person information (i.e., signal from visual perception) is crucial to generate the normal adult's understanding of social cognition and intersubjectivity.

As predicted, the left inferior parietal cortex also plays a special role in our imitation conditions. Activation of the left inferior parietal lobule in the contrasts involving Imitation of the other (A–C and A–D) fits neatly with its role in visuomotor integration for goal-directed actions. Lesions in this area are frequently associated with apraxic disorders, including impairment in imitation (Goldenberg, 1999) and impairments in motor imagery, that parallel impairments in praxis production (Ochipa *et al.,* 1997; Sirigu *et al.,* 1996). As illustrated in Fig. 2, the difference in parameter estimates in the left IPL is higher between conditions A and C or A and D than between A and B, which fits with its role in visuomotor control since conditions A and B imply a control of the action by watching matching manipulations performed by others, but only in condition A do subjects rely on the observation to act. This also explains its absence in the A–B contrast.

Parietal activity was found in the two contrasts described in Table 2, demonstrating that it cannot be explained by the absence of visual feedback of the action as in the case of the frontal areas. On the other hand, the clusters in both hemispheres are more restricted and lateralized when conditions of reciprocal imitation (A and B) are contrasted to Different action (D, Table 2) than to Self action (C, Table 1). The parameter estimates in Fig. 2 further illustrate that the increase in the right parietal lobule in situations of absence of feedback is specific to the imitation of the self by the other.

The right inferior parietal cortex is consistently activated when subjects watch other individuals' actions (Decety, 1997; Grèzes *et al.,* 1998). There is also plenty of evidence that the right inferior parietal cortex plays a key role in corporeal awareness, e.g., asomatognosia and hemineglect following lesion in this region (Mesulam, 1981; Berlucchi andAglioti, 1997). It is of special interest that one PET study has reported that schizophrenic patients who experience passivity phenomenon (i.e., the belief that one's thoughts or actions are being influenced or replaced by those of an external agent) showed hyperactivation of right inferior parietal during the performance of freely selected joystick movements in comparison to the response in normal subjects (Spence *et al.,* 1997). The authors argued that such abnormal response might prompt the misattribution of internally generated acts to external agencies. We thus suggest that the strong involvement of the right inferior parietal lobule is critical for the attribution of the action performed by the subject to the other when he is imitating the model (see Fig. 2).

CONCLUSION

The main result of this study is the differential activity in the inferior parietal cortex related to the two conditions of reciprocal imitation. The left inferior parietal is specifically involved in the imitation of the other by the self, whereas the right homologous region is more activated when the self imitates the other. This region may play a fundamental role in agency, i.e., in attributing the source of the action to self or other. Several recent studies have started to accumulate evidence, both in psychiatric patients (e.g., Spence *et al.,* 1997) and in normal subjects (e.g., Ruby and Decety, 2001; Ben Shalom, 2000), supporting this hypothesis. Similarly, the posterior part of the superior temporal gyrus also shows a differential activity, which could be involved in monitoring the first-person and third-person visual information. Over all, these results favor the interpretation of a lateralization in the posterior part of the brain related to self-related versus others-related information, respectively in the dominant versus the nondominant hemisphere.

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