

# Does the End Justify the Means? A PET Exploration of the Mechanisms Involved in Human Imitation

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Received April 30, 2001

**Imitation is a natural mechanism involving perception–action coupling which plays a foundational role in human development, in particular to extract the intention from the surface behavior exhibited by others. The aim of this H<sub>2</sub><sup>15</sup>O PET activation experiment was to investigate the neural basis of imitation of object-oriented actions in normal adults. Experimental conditions were derived from a factorial design. The factors were: (a) is the stimulus event shown to subjects during observation of the model and (b) is the response manipulation performed by the subject. Two key components of human action, the goal and the means to achieve it, were systematically investigated. The results revealed partially overlapping clusters of increased regional cerebral blood flow in the right dorsolateral prefrontal area and in cerebellum when subjects imitated either of the two components. Moreover, specific activity was detected in the medial prefrontal cortex during the imitation of the *means*, whereas imitating the *goal* was associated with increased activity in the left premotor cortex. Our results suggest that for normally functioning adults, imitating a gesture activates neural processing of the intention (or goal) underlying the observed action.** © 2002 Elsevier Science

**Key Words:** action; imitation; neuroimaging; human; goal; intention.

## INTRODUCTION

Interest in imitation has burgeoned in cognitive neuroscience, developmental psychology, evolutionary biology, and artificial intelligence. It is considered by many theorists as a foundational element in the evolution of culture and the ontogenetic development of intersubjectivity in *Homo sapiens* (e.g., Tomasello *et al.*, 1993). The developmental work indicates that imitation involves an innately based mechanism and that infant imitation is goal-directed and purposeful (for a recent review see Meltzoff and Moore, 1997). The cur-

rent study seeks to explore the neural substrate involved in specific aspects of imitation.

Neurophysiological evidence for a tight neural coupling between seen and performed actions has accumulated during the past decade. Fadiga *et al.* (1995) recorded motor-evoked potentials (MEPs) from intrinsic and extrinsic hand muscles elicited by transcranial magnetic stimulation (TMS) in subjects requested to observe grasping movements performed by an experimenter. At the end of the observation period TMS was applied to their motor cortex and motor-evoked potentials were recorded from hand muscles. The pattern of muscular response to this stimulus was found to be selectively increased in comparison to control conditions, demonstrating an increased activity in the motor system during the observation of actions. Several functional neuroimaging studies of action observation have already been conducted. Results showed that observation of someone else's action for later imitation is associated with activation in the same parietal and premotor regions that are involved in producing actions (Decety *et al.*, 1997; Grèzes *et al.*, 1998, 1999). This has led to the proposal that, during observation of action, the neural network subserving motor representations is already tuned for imitation. Recently, an fMRI study also demonstrated that action observation activates premotor cortex in a somatotopic manner (Buccino *et al.*, 2001).

Another set of data comes from monkey cell recordings. A number of studies, reviewed in Rizzolatti *et al.* (2001), have identified mirror neurons in the ventral premotor cortex of monkeys (area F5) as neurons active both when the monkey performs a particular action and when he sees the same actions performed by another individual, monkey, or human. It has recently been shown that half of the recorded mirror neurons in area F5 also responded when the final part of an action was hidden and could only be inferred (Ulmittà *et al.*, 2001) reinforcing the hypothesis that these neurons could code the goal of an observed action. The mirror system could therefore orchestrate the different components involved in the sensorimotor transformations

required by imitation, and area F5 would play a central role in a possible model of imitation (Arbib *et al.*, 2000).

The human homologue of F5 is believed to be Broca's area (left inferior frontal and gyrus), which would have similar mirror properties (see Rizzolatti *et al.*, 2001). Indeed, an fMRI performed by Iacoboni *et al.* (1999) found this area during single finger movement copying. However, because the nature of the movements, we think that the study of imitation of higher-level actions is necessary to argue for or against both the mirror neurons hypothesis and their localization in humans. Moreover, a recent meta-analysis performed by Grèzes and Decety (2001) on numerous neuroimaging studies dealing with action generation, simulation, and observation led the authors to postulate other possible alternatives for the location of the human homologue of the monkey area F5, in particular the ventral premotor cortex. A PET experiment was conducted by our group in order to identify the hemodynamic response to mutual imitation between the observer and experimenter. The right inferior parietal lobule, the superior temporal region bilaterally, and the medial prefrontal cortex were specifically activated in imitation conditions compared to matched, nonimitative action performances (Decety *et al.*, 2001).

Neuropsychological studies support the idea of a direct pragmatic route in the brain from vision to object-directed action. For example, patients with temporal damage and impaired semantic knowledge of objects can decide how an object should be used even when their semantic judgments about the objects are impaired (Hodges *et al.*, 1999; Humphreys and Riddoch, 2001). Conversely, patients with lesions of the posterior parietal cortex are impaired in calibrating the size and orientation of their grasp, although they have no difficulties in reporting the size and orientation of these objects or in discriminating between them (Goodale, 1997). It is thus acknowledged that a pragmatic route for object-related actions involves the posterior parietal cortex.

Taken as a whole, the existing literature strongly suggests that observing actions directly activates a matching motor program in the viewer (which could explain some forms of motor imitation) and that the perception of objects activates a motor program whose goal is the correct use of this object. Moreover, developmental research indicates that the distinction between matching an observed motor program (the *means* of the model) and reproducing the correct use of an object (the *goal*) is deeply rooted in human cognition. For example, even 18-month-old children have no difficulty in distinguishing the surface behavior of people (what they actually do, the *means*) from another deeper level (what they intend to do, the *goal*) as demonstrated by Meltzoff (1995) using a reenactment procedure. There is also evidence showing that imitation is mediated by a goal representation in slightly older

TABLE 1

2 × 3 Factorial Design Used to Explore Imitation of the *Goal* and the *Means*

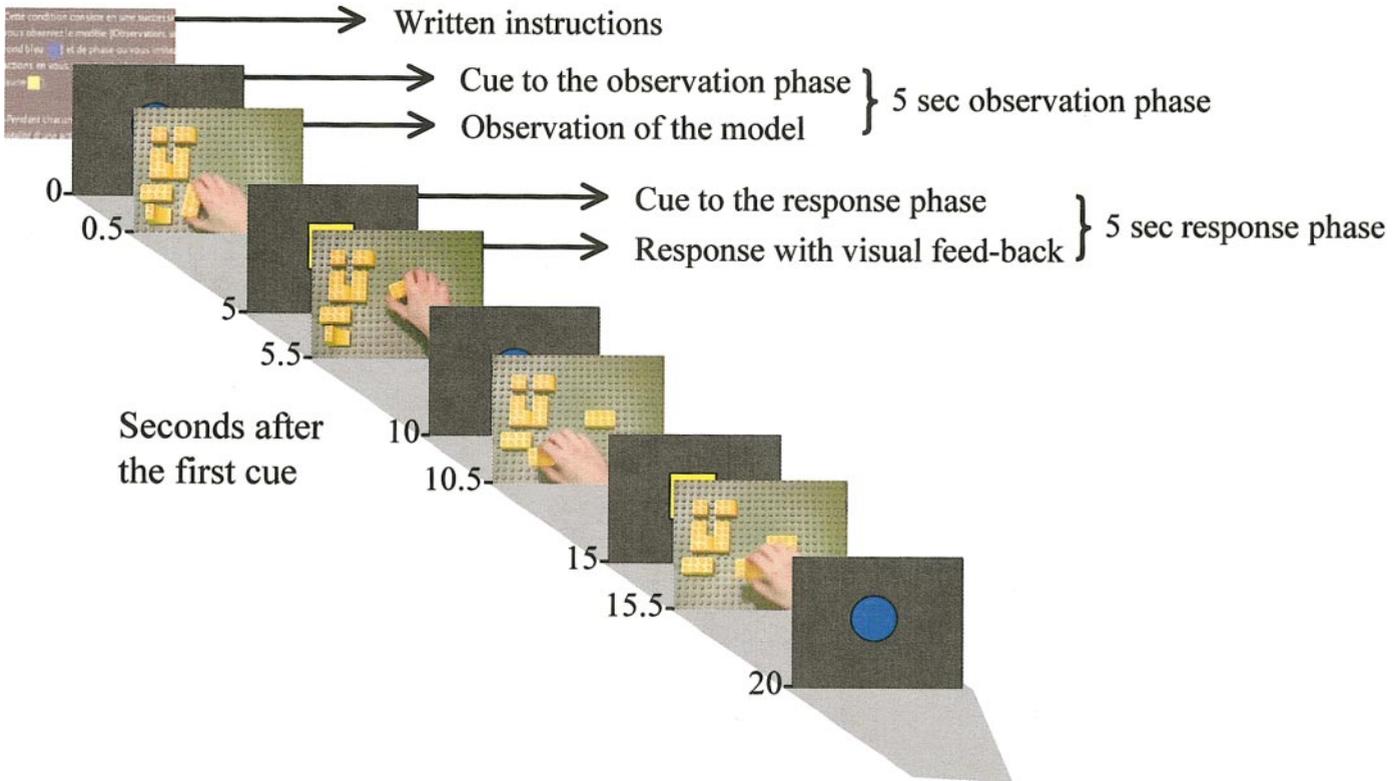
Observation	Response	
	<i>Imitation</i>	<i>Free action</i>
<i>Whole action</i>	IW	FW
<i>Goal of action</i>	IG	FG
<i>Means to achieve action</i>	IM	FM

Note. There were six activation conditions.

children. Bekkering *et al.* (2000) investigated preschool children in imitation tasks involving a set of contralateral and ipsilateral hand actions of varying complexity. They demonstrated that the accuracy of mapping of perceptual information to motor schemas was influenced by the goals of the actions. Children were more attuned to the reproduction of the *goal* (such as touching one of their ears or of a pair of dots on the table) than in the imitation of the precise *means* used (such as using the right or left hand). Their results suggest that the imitative act is directed or organized by the *goal* of the model.

Our aim was to use an imitation paradigm to differentiate the neural correlates of two implicit ways to retrieve action, either from the observation of its *means* or by referencing to the *goal* in the use of an object. Although there is no clear-cut division in ecological situations (Whiten and Ham, 1992), the *goal* can be operationalized in this experiment as the end state of the object manipulation, and the *means*, as the motor program used to achieve this relation. As suggested by Bekkering and Wohlschläger (2001), physical goals are represented in certain neural codes, which affect the selection of action during imitation.

The neural bases of the imitation of the *goal* and of the *means* of object-directed actions were explored by recording the variations of the regional cerebral blood flow (rCBF) during the imitation of object-directed actions. These actions consisted of manipulation of Lego blocks in order to build small constructions. We used a factorial design in which the six activation conditions corresponded to the crossing of two factors (see Table 1): (a) is the stimulus event shown to subjects during the observation of the model (*whole act*, *means alone*, *goal alone*) and (b) the response manipulation performed by the subject (*imitation* or *freely selected act*). The factorial design therefore explored the neural activity when one aspect of the action was hidden from the subjects when compared to the natural situation in which the whole action was shown. In these conditions, subjects were implicitly requested to work out the aspect of the act that was hidden from them (either the *goal* or the *means*) in order to reproduce it. Our assumption was that reproducing an action in which

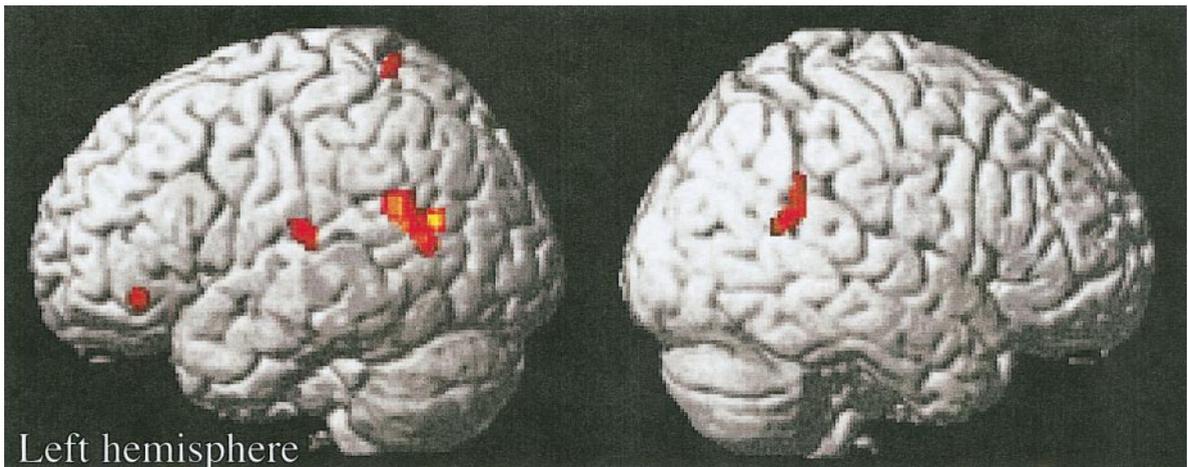


**FIG. 1.** Schematic representation of all conditions' organization. They started with a written reminder of the condition's instructions, followed by eight similar 10-s sequences consisting of the succession of a phase of observation of the model (4.5 s) and of a phase of response by the subject with visual feedback (4.5 s). Each phase was cued by a specific 0.5-s screen.

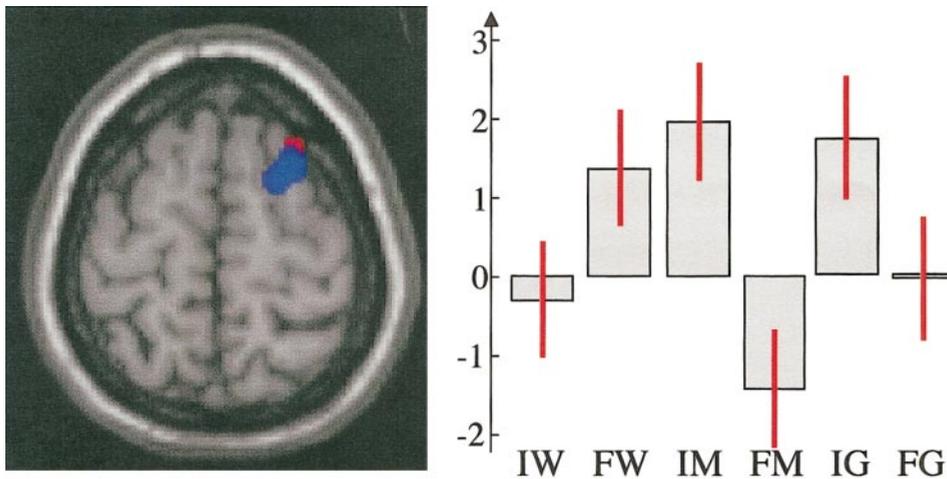
either the goal or the means were hidden from the subjects would engage specific cognitive strategies relying on specific brain networks. However, what differed between the conditions is what was explicitly shown to the subjects, and this was used to describe the conditions throughout the paper.

To our knowledge, this is the first functional neuroimaging study that differentiated the global act of im-

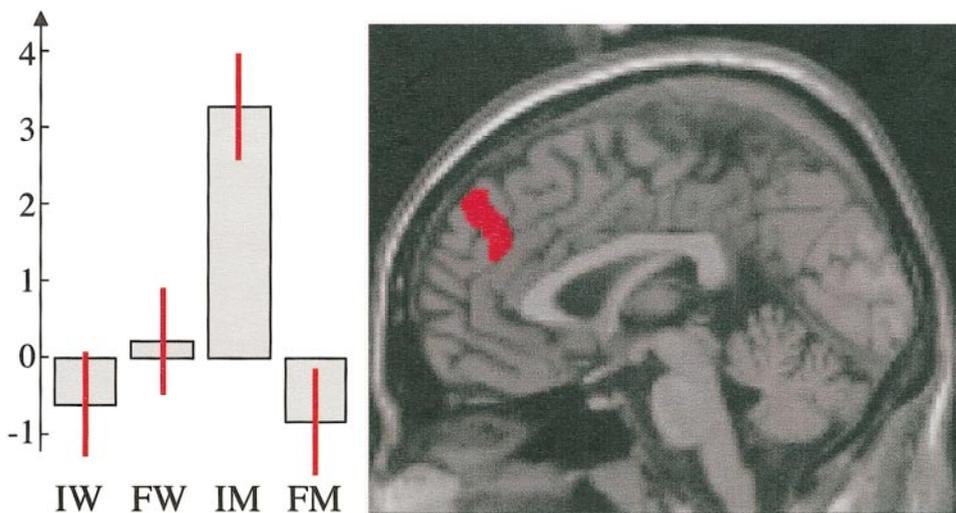
itation and systematically investigated the neural correlates of two complementary subspects of imitation—the goal of the act and the means to achieve it. Our hypothesis was twofold. First, *imitation* should selectively engage prefrontal and parietal areas, and two differentiable neural mechanisms should be involved. More precisely, the interaction between *imitating* and observing only the *goal* should preferentially



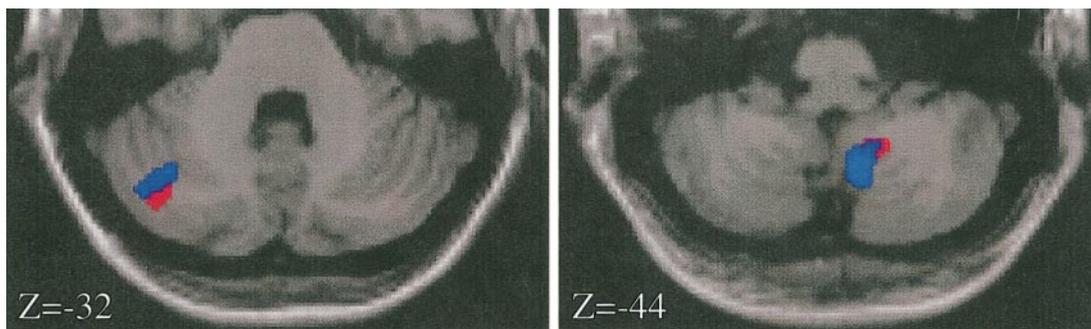
**FIG. 2.** Lateral render of a standard brain with superimposed foci of activity associated with the main effect of imitation (see Table 2).



**FIG. 3.** (Left) overlapping foci of activity in the right DLPFC associated with the two interactions described in Table 4 superimposed to standard horizontal section ( $z = 62$ ). Blue shows the effect of imitating the goal, and red, of imitating the means. (Right) Condition-specific parameter estimates in a voxel ( $x 30, y 16, z 64$ ) representative of the overlapping area.



**FIG. 4.** (Left) Condition-specific parameter estimates in a voxel ( $x 2, y 52, z 44$ ) representative of the activation in the medial prefrontal cortex in the interaction describing the imitation of the means. (Right) activated cluster superimposed to a parasagittal section.



**FIG. 5.** Partially overlapping foci of activity in the left lateral cerebellar hemisphere (on the left) and in the right medial cerebellum (on the right) associated with the two interactions described in table 4 superimposed to horizontal sections of the cerebellum.

activate the prefrontal areas thought to be involved in higher level cognitive tasks and between *imitating* and observing only the *means* would engage more posterior areas linked to the control of the action in space. Second, we postulated that *imitation* of the *goal* would preferentially activate areas involved in the retrieval of motor plans from the representation of the other's intention (premotor areas), whereas *imitation* of the *means* would require areas involved in the retrieval of the goals to which they were pointing. Thus, the medial prefrontal areas, that are acknowledged to be involved in mentalization tasks (results reviewed in Shallice, 2001; Blakemore and Decety, 2001) or alternatively Broca's area according to the mirror neurons hypothesis (Rizzolatti *et al.*, 2001), could play this role. We therefore had strong *a priori* hypothesis concerning the cortical regions involved.

## MATERIAL AND METHODS

### Subjects

Ten right-handed healthy male volunteers were recruited ( $24.2 \pm 2.9$  years). All subjects gave written informed consent according to the Helsinki declaration and were paid for their participation. The study was approved by the local Ethics Committee (CCPPRB, Centre Léon Bérard, Lyon, France).

### Activation Paradigm

Subjects were scanned during six conditions (IW, IM, IG, FW, FM, and FG, see Table 1) that were duplicated once (i.e., 12 scans per individual). The order of these six conditions was randomized within and between subjects. Each activation condition lasted 80 s and consisted of a succession of "observation phases" and "response phases" (Fig. 1). In each observation phase, the subjects watched a video clip showing a model's right-hand manipulation of one Lego block; in each response phase subjects were presented with similar Lego blocks and were required to make a similar right-hand action with direct visual feedback. A specially constructed workspace was used. It consisted in a Lego plate ( $40 \times 40$  cm) positioned above the subjects' chests at a comfortable distance for easy manipulation of Lego blocks. Subjects were trained to the manipulation of the Lego blocks in the PET environment prior to the scanning session.

A camera recorded the subject's workspace in the same orientation toward the hands and with the same angle as the model shown in the video clip. A video system allowed projection of the model's actions (in the observation phase) and of the subjects' actions (in the response phase) on a transparent screen positioned at the back of the PET scanner. A mirror was placed in front of the subjects' eyes in the PET scanner so that

they could see the video signals projected on the back screen. The resultant distance from the eyes to the screen was 50 cm approximately (corresponding field of view  $42^\circ$  in the horizontal dimension and  $32^\circ$  in the vertical one).

### Experimental Conditions

The experimental conditions differed in the two factors of interest (see Table 1). The first factor corresponded to the content of the films shown during the observation phase. There were three levels of this factor: (a) the *whole* motor act performed by the experimenter; (b) the hand gesture without the end-state, i.e., the hand of the model choosing, grasping, and moving the Lego block (the *means*); or (c) the final stage of the action performed by the experimenter, i.e., the hand of the model leaving the Lego block that has been placed in its end state (the *goal*). The second factor corresponded to the subjects' response and had two levels. The source of their actions was either internal (the subjects *freely select* the block movement they perform) or external (the subject *imitate* by reproducing the block movement demonstrated by the model).

*IW: Imitation of the whole action.* During each observation phase, subjects were shown a *whole* manipulation of the model on one Lego block. During each response phase, subjects had to *imitate* this manipulation.

*IG: Imitation of the goal of the action.* During each observation phase, subjects were only shown the *goal* of the model's action on one Lego block. During each response phase, subjects had to perform a block manipulation in order to achieve the same end state of Lego blocks.

*IM: Imitation of the means of the action.* During each observation phase, subjects were only shown the *means* of the model's action on one Lego block. During each response phase, subjects had to perform a block manipulation reproducing the gesture they had observed.

*FW: Free response after observation of the whole model's action.* During each observation phase, subjects were shown a *whole* manipulation of the model on one Lego block. During each response phase, subjects were allowed to perform block manipulation they freely chose.

*FG: Free response after observation of the goal of the model's action.* During each observation phase, subjects were only shown the *goal* of the model's action on one Lego block. During each response phase, subjects were allowed to perform a block manipulation they freely chose.

*FM: Free response after observation of the means of the model's action and free response.* During each observation phase, subjects were only shown the *means* of the model's action on one Lego block. During each

response phase, subjects were allowed to perform a block manipulation they freely chose.

### Subjects' Performance

Subjects' performance throughout all PET conditions were videotaped. The Lego constructions in the six conditions involving imitation were compared to those of the model. The number of errors in the selection and in the end-state position of the block for the eight block manipulations was counted. Results were statistically analyzed using one-way ANOVA and pairwise *t* tests.

### Stimuli Preparation

Ten different sequences of eight Lego blocks manipulation were recorded in the PET environment. Initial and end states of Lego block positions differed in all these sequences, and each of the 10 sequences was edited into each of the six conditions using computer-assisted video editing. The sequences used for the different conditions were counterbalanced between subjects.

For the video clips showing the *whole* action condition, all the components of each Lego block manipulation were shown (i.e., the hand choosing a Lego block, grasping it, moving it, placing it, and moving away). For the observation of the *goal*, only the last part of each block manipulation was shown (i.e., the hand moving away from the Lego block that has been placed). For the observation of the *means*, only the first parts of each Lego block manipulation were shown (i.e., the hand grasping and moving the Lego block). Sufficient information for reproducing the end state of the action was available in the video clips made for the observation of the *goal* and of the *means*. All these clips lasted 4.5 s and were designed to involve the same quantity of hand movement so that the visual input was similar across all conditions.

Subjects were prompted with written instructions that were inserted at the beginning of the video clip in each experimental condition. They were cued by a 0.5-s blue circle before each observation phase and by a 0.5-s yellow square before each response phase (see Fig. 1).

### Scanning Procedure

A Siemens CTI HR+ (63 slices, 15.2-cm axial field of view) PET tomograph with collimating septa retracted operating in 3D 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.

### Data Analysis

Images were reconstructed and analyzed with the Statistical Parametric Mapping software (SPM99, Friston *et al.*, 1995; Wellcome Department of Cognitive Neurology, UK; implemented in MATLAB 5 (Math Works, Natick, MA)). For each subject, images were realigned to the first scan then normalized into the MNI stereotaxic space. Data were convolved using a gaussian filter with a full-width half-maximum (FWHM) parameter set to 12 mm.

The design for statistical analysis in SPM was defined as "multisubjects and multiconditions" with 105 *df*. Global activity for each scan was corrected by grand mean scaling. The condition (covariate of interest) and subject (confound, fixed effect) effects were estimated voxelwise according to the general linear model. Linear contrasts were assessed to identify the significant difference between conditions, and were used to create an SPM  $\{t\}$ , which was transformed into an SPM  $\{Z\}$  map. The SPM  $\{Z\}$  maps were thresholded at  $P < 0.005$  for main effect analysis and at  $P < 0.001$  for interaction analysis. Condition-specific parameter estimates reflect the adjusted rCBF relative to the fitted mean and expressed as a percentage of whole brain mean blood flow in a voxel of an activated cluster. Anatomical identification was performed with reference to the atlas of Duvernoy (1991).

## RESULTS

Two factors were manipulated in this PET activation study. The first factor was related to observation of the model and subjects were shown either a *whole* manipulation of Lego block, only the *goal* of the action, or only its *means*. The second factor was the actual performance of an action by the subject, who was asked either to *imitate* the model's manipulation or to *act freely* on any of the objects.

A one-way analysis of variance on the subjects' performance in *imitation*, coded as the number of errors for the eight manipulations performed during one condition, revealed a significant main effect of the observation factor ( $F(2,30) = 19.1$ ,  $P < 0.0001$ ). Subjects performances were near ceiling levels in the *imitation* of the *whole* condition (IW,  $M = 0.05$  errors,  $SD = 0.05$ ). Pairwise comparisons revealed significantly more errors in the *imitation* of the of the *goal* (IG,  $M = 0.65$ ,  $SD = 0.20$ ) compared to the whole condition,  $t = 3.04$ ,  $P < 0.01$ ; and more errors in the *imitation* of the *means* (IM,  $M = 1.45$ ,  $SD = 0.21$ ) compared to the *whole*,  $t = 5.98$ ,  $P < 0.001$ ; there was no significant difference in *imitation* of *means* compared to *goal* ( $t = 2.62$ ,  $P > 0.01$ ).

TABLE 2

Regions of Increased Brain Activity Associated with the Main Effect of *Imitation* Compared to Free Selection of Action [(IW - FW) + (IM - FM) + (IG - FG)]

Brain region	MNI coordinates			Z score
	x	y	z	
L superior parietal lobe	-18	-50	70	3.75
R inferior parietal lobule	68	-50	22	4.03
L inferior parietal lobule	-64	-54	20	4.62
L posterior superior temporal sulcus (STS)	-42	-64	16	4.38
L superior temporal gyrus	-60	-20	14	3.81
L lateral orbital gyrus	-52	36	-10	4.02

Note. Voxel threshold 15,  $P < 0.0005$ . L, left hemisphere; R, right hemisphere.

Analysis of the neuroimaging data resulted in the creation of statistical parametric maps in accordance with the factorial design used. Simple effects were calculated to confirm the directionality of the interactions and the statistical value of the differential activities between them.

The main effect of *imitation* [(IW - FW) + (IM - FM) + (IG - FG)] showed bilateral increased activity at the border between the posterior superior temporal gyrus and the inferior parietal lobule, as well as in the ventral prefrontal cortex, the superior temporal gyrus, and the superior parietal lobe (Table 2 and Fig. 2) in the left hemisphere. Subsequent analysis of the condition-specific parameter estimates showed two areas strongly associated to *imitation* in this paradigm, in the lateral orbitofrontal cortex and inferior parietal lobe in the left hemisphere.

The main effect of *free selection of action* [(FW - IW) + (FM - IM) + (FG - IG)] showed areas of activation in the anterior cingulate, in the inferior temporal lobe, and in the dorsolateral prefrontal cortex in both hemispheres as well as in the left superior parietal lobe, more posterior than the region indicated in Table 2.

The observation of only the *goal* of other's actions contrasted with the observation of the *whole action* led to activation in the dorsolateral prefrontal cortex, the superior parietal lobe, and the anterior cingulate gyrus in the right hemisphere and in the orbitofrontal, supramarginal, and middle temporal gyri in left hemisphere. The observation of only the *means* of other's actions contrasted to the observation of the *whole action* led to activation in the medial prefrontal cortex, the inferior parietal lobe, and the middle frontal gyrus bilaterally, as well as in the left middle temporal gyrus and the right anterior temporal lobe (Table 3).

Specific areas showed preferential activation to an interaction between the two experimentally manipu-

TABLE 3

Regions of Increased Brain Activity Associated with the Main Effect of Observation of the *Goal* of Action or of Its *Means* Compared to Observation of the *Whole* Action

Brain region	MNI coordinates			Z score
	x	y	z	
Observation of the goal [(IG - IW) + (FG - FW)]				
R dorsolateral prefrontal cortex	38	8	64	4.56
R superior parietal cortex	50	-74	42	4.37
L supramarginal gyrus	-52	-56	34	3.86
R anterior cingulate gyrus	12	26	34	4.01
L middle temporal gyrus	-60	-46	-2	4.96
L orbitofrontal	-26	44	-12	3.79
Observation of the means [(IM - IW) + (FM - FW)]				
L medial dorsolateral prefrontal	-14	22	64	4.92
R medial dorsolateral prefrontal	8	22	54	3.99
R angular gyrus	66	-58	38	4.29
R middle frontal gyrus	26	54	36	4.03
L supramarginal gyrus	-54	-62	32	4.82
R anterior cingulate gyrus	4	26	22	3.91
L middle frontal gyrus	-30	54	8	4.28
L middle temporal gyrus	-60	-46	2	4.50
R anterior temporal lobe	56	14	-18	4.11

Note. Voxel threshold 15,  $P < 0.0005$ .

lated factors, i.e., observation and response (Table 4). The first interaction [(IG - FG) - (IW - FW)] reflects the effect of observing only the *goal* of behavior during the *imitation* tasks. There was significantly more activity in prefrontal cortex and in the cerebellum bilaterally. The second interaction [(IM - FM) - (IW - FW)] reflects the effect of observing only the *means*

TABLE 4

Regions of Increased Brain Activity in the Interaction Showing the Interaction Effect of *Imitating* with Observation of Only the *Goal* or Only the *Means* of the Model's Actions

Brain region	MNI coordinates			Z score
	x	y	z	
Imitation with observation of only the goal [(IG - FG) - (IW - FW)]				
R dorsolateral prefrontal cortex	28	12	64	4.31
L prefrontal cortex	-52	8	42	4.15
L lateral cerebellum	-40	-68	-34	3.50
R medial cerebellum	10	-58	-42	3.93
Imitation with observation of only the means [(IM - FM) - (IW - FW)]				
R dorsolateral prefrontal cortex	28	18	66	3.55
Medial prefrontal cortex	2	52	44	3.38
L lateral cerebellum	-38	-72	-34	3.57
R medial cerebellum	14	-54	-42	3.48

Note. Voxel threshold 15,  $P < 0.001$ .

used to achieve the behavior during the *imitation* tasks. Increased rCBF was detected in the cerebellum bilaterally, in the medial prefrontal cortex (condition-specific parameter estimates in the six conditions is shown in Fig. 3) and in the right dorsolateral prefrontal cortex (DLPFC). The two interactions yielded partially overlapping clusters of activity in the right DLPFC (see Fig. 4) and in the right lateral and left medial cerebellum (see Fig. 5). The directionality of these interactions was assessed by computing simple effects between the conditions of interest, IG and IM, and their control IW. The first contrast yielded significant effects,  $P < 0.0005$ , with the expected clusters located in the right DLPFC ( $x = 36, y = 8, z = 64$ ), the left premotor cortex ( $-52, 10, 44$ ), and the right medial ( $14, -76, -36$ ) and left lateral cerebellum ( $-36, -66, -42$ ), as well as clusters already described as resulting from the observation effect. Similarly, the second contrast (IM - IW) showed rCBF increase in the medial prefrontal cortex ( $4, 22, 54$ ) and the right medial ( $16, -52, -42$ ) and left lateral cerebellum ( $-40, -72, -36$ ), as well as clusters already described as resulting from the observation effect.

In addition, a direct comparison of the two conditions of interest, namely IG and IM, was performed to confirm the differential involvement of brain areas described in the two interactions. The simple effect IG - IM at  $P < 0.0005$  confirmed the involvement of the left premotor ( $-20, 16, 54$ ) in the imitation of the goal when compared to imitation of the means. A cluster ( $22, 6, 60$ ) was found in the vicinity of the right DLPFC overlapping foci described in the interactions (Fig. 4). The inverse contrast (IM - IG,  $P < 0.0005$ ) confirmed the involvement of the medial prefrontal cortex ( $2, 56, 36$ ). These contrasts also revealed a differential involvement in the partially overlapping cerebellar foci found in the two interactions. RCBF increase was found in medial cerebellum in IG - IM ( $12, -76, -36$ ), and in the left lateral cerebellum in IM - IG ( $-38, -78, -36$ ).

## DISCUSSION

Although no clear-cut distinction exists between copying the behavior or its results in most ecological situations our experiment was designed to investigate neural correlates of these two complementary subcomponents of goal-directed actions.

The main effect of imitation showed parietal regions, known to be involved in higher-order motor representations and sensorimotor transformations. It also involved the posterior STS, which is compatible with its functional role in perception of actions, both in nonhuman (Jellema and Perrett, 2001) and human primates (Allison *et al.*, 2000; Blakemore and Decety, 2001). Since these areas were detected when contrasting two sets of conditions involving similar action observation

and object manipulations, it is unlikely that they were simply engaged in the motor component of the imitation task. It is more likely that they are associated with the cognitive process of imitation. These experimental findings fit well with clinical observations of apraxic patients who are impaired in action imitation after lesion in the inferior parietal region (Goldenberg *et al.*, 1996; Halsband *et al.*, 2001). They are also consistent with a recent PET study of our group that has shown activation in both posterior temporal gyrus and inferior parietal lobule during reciprocal imitation (Decety *et al.*, 2002). We proposed that the left STS is concerned with the analysis of the other's actions in relation to the self's motor intention.

The activation in the inferior part of the frontal lobe lies in the lateral orbital gyrus. It has been suggested that the orbitofrontal cortex is activated when there is insufficient information available to determine the appropriate course of action (Elliot *et al.*, 2000). In the present study, there was always an uncertainty for the subject concerning the end-state Lego construction made by the experimenter, which could well account for this effect. Alternatively, and taking into account the limited spatial resolution of PET, it could be argued that this orbitofrontal cluster in fact lies in the anterior part of the inferior frontal gyrus. The activity found in the left superior temporal, the inferior parietal, and inferior frontal cortices is congruent with data from monkeys (Jellama and Perrett, 2001) and humans (reviewed in Rizzolatti *et al.*, 2001) indicating a key role to these regions in imitation.

Observation of the means and of the goal of actions performed by the model was associated with common foci of increased activity in the left inferior parietal lobule, the left middle temporal gyrus, and in the anterior cingulate gyrus. Interestingly, these regions were found to be engaged even though observation of the whole gesture was subtracted, and all conditions were normalized for the quantity of hand movements. This indicates that removing information about other's actions, whether it is goal or the means used, more strongly involves the regions that are necessary for the visual analysis of purposeful hand movements than the whole action. Moreover observation of both the goal and the means necessitate a similar analysis of the visual input. Different activated foci in the two main effects of observation were found in the prefrontal cortex in its medial and dorsolateral part for the observation of the means and of the goal, respectively.

In a factorial design, interactions allow us to assess the effect of one factor, what is observed by the subject, on the effect of the other, imitating. They permit the identification of brain areas related to the imitation when only the means or the goal of the model are observed, irrespective of the action performed and observed by the subject. Statistical analysis of the subjects' performances shows no difference in the number

of mistakes between imitating of the goal and imitating of the means of the action, even though there is a statistical increase in errors when these conditions are compared to imitation of the whole action. Subjects' performances therefore argue in favor of a comparison of the two interactions of interest.

The interaction effects demonstrated that there was significantly more activity in cerebellum and in the frontal cortex when only partial information about the model's action is available for imitation. Activated areas in the two interaction effects did not overlap with those described in the main effect of imitation, which suggest that they cannot be explained by the neural activity associated with motor control. These activated areas were also different from the parietal and temporal areas found in the two main effects of observation, implying that they cannot be explained by an effect of observation. Therefore, we suggest that the activity of these frontal areas reflects the transformation of the partial information from the model into a complete action that must be performed by the subject.

Interestingly, the activated clusters revealed by the interactions partly segregate. While the right dorsolateral prefrontal cortex was detected for both the goal and the means, the medial prefrontal cortex was only found in imitation of the means, and the left premotor cortex, for the goal. The finding of the involvement of the right dorsolateral prefrontal cortex fits with its critical role in the preparation of forthcoming action based on stored information (Pochon *et al.*, 2001). This region was more activated during the interaction describing the imitation of the goal, which leads us to suggest that it stores the representation of the goal in short-term working memory. Therefore, its activation during imitation of the means suggests that this condition stimulates the representation of the goal that is built from the observed gesture (Miller, 2000). The fact that imitation of the means activates a representation of the goal fits nicely with the fundamental goal-directedness of imitation in children emphasized by developmental psychologists (Bekkering *et al.*, 2000; Gleissner *et al.*, 2000).

The medial prefrontal region is known to play a critical role in reading others' intentions (for a review see Shallice, 2001). Its activation, only found in the imitation of the means, may reflect the retrieval of the goals or intentions of the actor from the observation of his gestures. It thus confirms that the extraction of simple action goals (as in our study) and the extraction of much higher-order intentions (as in the review by Shallice, 2001) are deeply related at several levels of analysis—developmental (Meltzoff, 1995; Meltzoff and Brooks, 2001; Bekkering *et al.*, 2000), theoretical (Bekkering and Wohlschläger, 2001), and neural (Blake-more and Decety, 2001).

The premotor cortex is acknowledged to play a role in several aspects of the preparation of action (Krams *et*

*al.*, 1998; Schluter *et al.*, 1999). Since the actions produced were similar in all conditions, the premotor activity associated with the imitation of the goal (in the interaction and the two simple effects) implies that the preparation of a given goal-directed action is cognitively more demanding when the associated gestures, the means, are not presented in the stimulus array for observation. It is now accepted that the observation of actions activates areas involved in the preparation of action (Grèzes and Decety, 2001), including the premotor cortex (Buccino *et al.*, 2001), and it has been proposed that this activation could tune the motor system for later imitation (Decety *et al.*, 1997). Therefore, one key difference between imitating after observing only the goal or only the means of an action could be that in the latter situation, the motor system is already prepared by the observation to reproduce the action, whereas in the former, the whole forthcoming action must be prepared to achieve a given goal.

Alternatively, the premotor activity resulting from the interaction between imitation and observation of only the goal could be explained by the proposed mirror properties of the premotor area (Buccino *et al.*, 2001). In monkeys, the premotor system is believed to code the goal of an action, which could explain why this area is present in the interaction describing imitation when only the goal is shown and not when only the means are shown. However, this interpretation does not explain our results since the interaction involved subtracting imitation of a complete action (IW – FW) from the imitation with observation of only the goal (IG – FG). Therefore, all effects linked to the observation of the goal should be removed. We therefore argue that this activity is due to the absence of observation of the means, which implies a reconstruction of the unseen action. The finding of an activity of premotor neurons in the monkey when the goal of the action is hidden (Umiltà *et al.*, 2001) fits well with this interpretation since it shows that observation of the means of an action activates brain structures involved in the observation of the whole action as well as with the production of the same action.

The two interaction effects reveal the involvement of three critical cortical areas the right dorsolateral prefrontal, the medial prefrontal, and the left premotor cortices. These seem to be involved respectively in storing a representation of the goal, retrieving the goal from the observation of an object-directed action, and preparing the forthcoming action.

At a computational level, imitation of complex behavior can be understood as the generation of internal models of action from a set of sensory inputs on the one hand and from movements experienced in the past on the other hand (Arbib *et al.*, 2000). It has been proposed that both inverse and forward internal models are used for motor planning (Wolpert and Kawato, 1998) and the cerebellum has been postulated to com-

pute both (Wolpert *et al.*, 1998; Imamizu *et al.*, 2000; Blakemore *et al.*, 2001). Inverse models provide the motor commands necessary to achieve a desired state and could be more implicated in the imitation of the goal while forward models act as predictor of the next state of an action and could be used for the estimation of the intended goal from the observation of other people's action (Blakemore and Decety, 2001). Our results show partially overlapping clusters in the left lateral horizontal fissure and in the right medial cerebellum in the two interaction effects. Moreover, a cluster located in the vicinity of the medial cerebellar overlapping area was found in the IG – IM contrast, therefore specific to imitating the goal, as well as a cluster in the left lateral horizontal fissure in IM – IG, specific to imitating the means. Our results could therefore reflect a different neurophysiological substrate within the cerebellum for the two types of models as suggested by Wolpert *et al.* (1998).

In sum, the results of this study suggest that the global category of imitation can partly be subdivided into complementary aspects, namely the goal of an action and the means to achieve it. The results identify neural correlates of these aspects, corroborating related behavioral findings in the developmental (Bekkering *et al.*, 2000; Meltzoff, 1995), comparative (Byrne and Russon, 1998; Whiten 1998), and clinical neuropsychological (Halsband *et al.*, 2001) domains. The current study also demonstrates that imitation is a creative reconstruction of observed action since imitation of the means activates a representation of the goal that was not physically present in the observed stimulus but only “implied.” This supports the idea that when observing someone's action, the underlying intention is equally or perhaps more important than the surface behavior itself (Baldwin and Baird, 2001; Meltzoff, 1995).

## ACKNOWLEDGMENTS

This research was supported by the “Programme Cognitique” from the French Ministry of Education (J. Nadel P.I.). Additional support is also gratefully acknowledged from NICHD (HD-22514) and the Talaris Research Institute. Dr. S.-J. Blakemore provided valuable input in all stages of this study.

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