

# TOP-DOWN EFFECT OF STRATEGY ON THE PERCEPTION OF HUMAN BIOLOGICAL MOTION: A PET INVESTIGATION

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This experiment was designed to investigate the neural network engaged by the perception of human movements using positron emission tomography. Perception of meaningful and of meaningless hand actions without any purpose was contrasted with the perception of the same kind of stimuli with the goal to imitate them later. A condition that consisted of the perception of stationary hands served as a baseline level.

Perception of meaningful actions and meaningless actions without any aim was associated with activation of a common set of cortical regions. In both hemispheres, the occipito-temporal junction (Ba 37/19) and the superior occipital gyrus (Ba 19) were involved. In the left hemisphere, the middle temporal gyrus (Ba 21) and the inferior parietal lobe (Ba 40) were found to be activated. These regions are interpreted as related to the analysis of hand movements. The precentral gyrus, within the area of hand representation (Ba 4), was activated in the left hemisphere. In addition to this common network, meaningful and meaningless movements engaged specific networks, respectively: meaningful actions were associated with activations mainly located in the left hemisphere in the inferior frontal gyrus (Ba 44/45) and the fusiform gyrus (Ba 38/20), whereas meaningless actions involved the dorsal pathway (inferior parietal lobe, Ba 40 and superior parietal lobule, Ba 7) bilaterally and the right cerebellum. In contrast, meaningful and meaningless actions shared almost the same network when the aim of the perception was to imitate. Activations were located in the right cerebellum and bilaterally in the dorsal pathway reaching the premotor cortex. Additional bilateral activations were located in the SMA and in the orbitofrontal cortex during observation of meaningful actions.

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Thus, when perception has no goal, the pattern of brain activation is dependent on the nature of the movements presented. But when perception has a goal, namely to imitate, the subject's strategy has a top-down effect on the information processing, which seems to give priority to the dorsal pathway involved in perception for action.

## INTRODUCTION

It is universally acknowledged that vision is the pre-eminent sense to gather information from the environment and that perception is the gateway to cognition. Among all visual inputs, perception of the behaviour of others is particularly and critically important in human social communication. Indeed, the determinants of behaviour are unequivocally and specifically linked to the pattern of body movements, from which intentions, emotions, or motives may be recognised and identified on a purely perceptual basis (Stränger & Hammel, 1996). Perception of biological movements is also the first step of imitation, a powerful means of establishing contact with other individuals and acquiring new skills from them, which starts very early in life (Meltzoff & Moore, 1977). It has been proposed that infants' primordial "like me" experiences are based on their understanding of bodily movement patterns and postures (Meltzoff & Gopnik, 1993). Imitation, which necessitates observation with the intention of immediate or later reproduction, may be regarded as an important link between perception and action. Indeed, imitation requires the perception and the storage of observed action as well as its transformation into the motor system (see Vogt, 1996).

Perception of biological motion has been extensively studied by psychologists, who have shown that humans can easily recognise actions, even from a limited number of visual cues. Johansson (1973) filmed a human actor moving in a dark room with lights attached to his main joints (shoulder, elbow, wrists, knees, and ankles). Filmed movement patterns of walking, cycling, climbing, and dancing by the point-light stimulus persons were not identified when lights were stationary but as soon as they were moving, they were quickly and easily recognised as human movements. This finding was extended by Cutting and Kozlowski (1977), who showed that subjects were able to identify friends by their gait as well as the gender of a walking person (Kozlowski & Cutting, 1977). Beardsworth and Buckner (1981) further demonstrated, from the point-light technique, that people can recognise themselves much more easily than others. This is a remarkable finding, since generally one perceives the movements of other individuals more frequently and more completely than one's own body movements. These observations were interpreted within the theory of Gibson (1979), which assumes that behaviour is an ecological event, whose recognition probably has biological survival value—namely, adaptation of the functions of the perceptual system to relevant structures in the environ-

ment. In this "direct perception" theory, invariant information given by the sizes, slants, and distances of surfaces surrounding the observer, through optic flow, dictates specific actions. Accordingly, this information has been termed an object's affordance. The detection of an affordance will lead directly to the appropriate action without the need to postulate a representational level. These experiments also demonstrate that the kinematic of movements is determinative of action recognition and even for the recognition of the intention (see Runeson & Frykholm, 1983).

Recent studies suggest that visual perception of actions could be influenced by implicit knowledge about the movements involved in their production. This hypothesis was supported by research on the visual perception of dynamic stimuli by Viviani and Stucchi (1992). One of the laws of graphic production specifies that the velocity of graphic movements involving the hand-arm system is a function of the curvature of the trajectory. In their experiment, Viviani and Stucchi presented a spotlight that traced an ellipse. The eccentricity of the ellipse was reduced progressively until the spotlight traced a circle, while the velocity profile of the first trajectory remain constant. Subjects tended to perceive an ellipse instead of a circle. This result shows that visual perception is constrained by knowledge on the law of graphic production. Thus, biological motion perception seems to rely on kinematic information of the movement perceived. This cannot be explained only in terms of visual experiences previously stored in memory. The idea that recognition processes are mediated by knowl-

edge of the underlying production rules is also supported by other studies. For instance, Orliaguet, Kandel, and Bøe (in press), performed a series of elegant studies in visual perception of motor anticipation in handwriting. The results demonstrated that the motor system anticipates the production of the forthcoming graphemic sequence during the production of the first letter. The study also showed that the visual system can exploit this anticipatory information to predict the second letter.

Neurophysiological evidence concerning the brain mechanisms that underlie the perception of biological motion is provided by several sources of converging, although different, approaches: electrophysiology in monkeys, clinical neuropsychology, and recently brain metabolic mapping in normal human subjects. The understanding of the neural substrate involved in the perception of biological motion is also important because it constrains cognitive theories.

A well-established general framework indicates that the visual cortex is organised into two distinct pathways, both originating in the primary visual cortex. The ventral stream that reaches the inferotemporal cortex is involved in the identification of objects, whereas the dorsal stream that projects into the parietal cortex is engaged in the visual spatial localisation of objects (Ungerleider & Mishkin, 1982). Recently, Milner and Goodale (1995) substantially reinterpreted these functions on the basis of neuropsychological dissociations. They postulated that both streams process information about object features and their spatial localisation, but that the visual information is used

differently by each stream. The ventral pathway would allow the construction of long-term perceptual representation from object features and their relations. These representations are implicated in the recognition, categorisation, and semantic representation of objects. In contrast, processes supported by the dorsal pathway concerns on-line information about the spatial location of objects. The dorsal stream and associated pathways are responsible for the programming and for the visual control of skilled movements. To summarise, the nature of the purpose of the perception (perception/action) determines the nature of the processing engaged (dorsal or ventral stream). For a recent review, see Goodale (1997).

### Electrophysiology in the Monkey

Two brain regions are known to be implicated in the perception of biological movements in the macaque monkey. These regions include specific areas located in the temporal and frontal lobes. Perrett and his co-workers (Perrett et al., 1989; Perrett, Mistlin, Harries, & Chitty, 1990) have discovered that in the anterior section of the superior temporal sulcus (STS) there are distinct neural populations which appear to be involved in visual recognition and understanding actions. One type of cells in the STS is selectively responsive to a particular type of body movement, taking into account information about the form of body components with information about the type of movements they are executing. Some of these neurons are re-

sponsive to the whole-body movements such as walking, and encode specific direction of motion. A second type of cells is selectively activated by the observation of goal-directed actions. These neurons show selectivity for specific hand-object interactions, such as reaching for, retrieving, manipulating, and holding; but do not respond to hand movements miming the action in the absence of the object, or when the hand and object are spatially separated by a few centimetres. Thus, these cells are sensitive to the causal relation between the agent performing the action and the object acted upon (Carey, Perrett, & Oram, 1997).

Another population of neurons located in the ventral lateral premotor cortex (F5) has similar interesting properties with respect to action perception. The similarities between the visual properties of F5 and the superior temporal sulcus neurons are striking. Both populations are sensitive to the hand-object interactions and their causal relation. However, a remarkable difference between these two populations is that neurons in F5 are firing both during the monkey's observation of a particular action executed by the experimenter or by another animal, and during the monkey's performance of the same action ("mirror neurons"; Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). According to Carey et al. (1997), the physiological results from STS and F5 indicate that there are brain processes in monkeys which could support the understanding of others' actions, and that the sight of these actions could be matched to the motor

commands in order to imitate or reproduce actions that monkey sees.

Another brain region involved in the visual analysis and control of action lies in the parietal cortex. Recent neurophysiological studies in alert monkeys have revealed that the parietal association cortex plays a crucial role in depth perception and in visually guided hand movement. Sakata, Taira, Kusunoki, Murata, and Tanaka (1997) suggested that neural representation of 3-D objects with real physical dimensions and their egocentric positions seems to occur in the parietal association cortex. The major purpose of the 3-D representation is the visual guidance of goal-directed action. However, as suggested by Carey et al. (1997), it is not clear whether cells within the parietal cortex code the sight of actions executed by other individuals or utilise such information to enable imitation or other types of interaction. The parietal cortex projects heavily to the premotor cortex with distinct connections between the superior parietal lobule and the dorsal portion of the premotor cortex and between the inferior parietal lobe and the ventral premotor cortex. The former is involved in action planning whereas the latter is involved in on-line control of action (Jackson & Hussain, 1996).

## Neuropsychology

It is worth considering the neurophysiological evidence in relation to observations of selective impairments in neurological patients. Of particular importance, neuropsychological studies on apraxia have raised interesting

dissociations, especially in ideomotor apraxia (De Renzi, 1989). Clinical observations have frequently reported that these patients have great difficulty in copying and/or recognising movements or gestures made by the experimenter or in executing such movements on verbal command. Apraxic patients with lesions that involve the parietal lobe are impaired in discrimination and comprehension of visually presented gestures, whereas patients with more anterior lesions (not affecting the parietal cortex) do not have difficulties in these tasks. All of these patients are deficient in gesture production. Liepmann (1977) writing in 1900, argued that "movement formulae" or memories that guide skilled movements are degraded in patients with parietal lesions and that this degradation produces an inability to perform or discriminate gestures. In contrast, when lesions are more anterior, these memories are undamaged, yet they cannot be used by the parts of the brain that are responsible for planning motor actions (premotor cortex, supplementary motor area [SMA], and prefrontal cortex). This latter case produced apraxia without impairments in gesture discrimination (Heilman, Rothi, & Valenstein, 1982).

Based on studies and observation on apraxic patients, Rothi, Ochipa, and Heilman (1991) developed a cognitive neuropsychological model of limb praxis and apraxia to account for dissociations on the one hand, between imitation and recognition (Rothi, Mack, & Heilman, 1986), and on the other hand, between imitation of meaningful and meaningless movements (Melner, 1987). This model is composed by an action input lexicon, which

has access into systems that contain the semantic knowledge of action and allows the identification, comprehension, and discrimination of gestures. The input action lexicon has also access to the output action lexicon, which contains time-space representation of skilled movements. These memories are later transformed into innervatory patterns (i.e. motor codes). In order to explain the dissociation between meaningful and meaningless gestures, as well as the ability to imitate meaningful action without comprehension, Rothi et al. (1991) suggested that gesture imitation could be performed from a nonlexical route, i.e. a direct route between the visual analysis and the innervatory patterns, without using the action lexicon.

### **Brain Metabolic Mapping**

PET offers privileged access *in vivo* to all areas in the brain that are engaged by biological motion. However, few PET studies have so far addressed this question. Bonda, Petrides, Ostry, and Evans (1996) investigated the perception of transitive hand action (i.e. imitating the act of reaching forward toward a glass and bringing it to the mouth) and of intransitive expressive movement of the whole body (i.e. to dance). These actions were recorded using the point-light technique. Subjects were required to carefully observe the moving dot-light because they would have to recognise the sequences that they previously observed. Perception of hand motion was associated with activations located in the left superior temporal cortex in its caudal extent, in the anterior

part of the left intraparietal sulcus (Ba 40) and bilaterally in the ventral temporo-occipital cortex (Ba 19/37). In contrast, whole body movements were associated with regional cerebral blood flow (rCBF) increases in the right middle section of the superior temporal sulcus, in the amygdaloid region in both sides, and in other limbic structures interconnected with the amygdala. The pattern of activated regions during hand-action was thought to play a role in the interpretation of instrumental actions, for which access to the left parietal lobe underlying body knowledge is required. In contrast, perception of whole-body actions involves interaction with the limbic system, which was inferred to be critical for the interpretation of expressive events.

A PET study performed by Rizzolatti et al. (1996) was designed to localise brain regions involved during observation of grasping movements. Subjects were scanned under three conditions. In the first, they had to observe grasping gestures of common objects performed by an experimenter. In the second, subjects had to reach and grasp the same objects. The third condition, consisting of object observation, was used as a reference level for comparison with the other activation conditions. Brain areas engaged during grasp observation were located in the middle temporal gyrus (Ba 21) and in the caudal part of the inferior frontal gyrus (Ba 45). On the basis of monkey data, Rizzolatti and co-workers (1996) argued for the functional homology between Brodmann area 21 in man and STS, in which neurons are activated by object features and also by the sight of actions performed by the

hand (Perrett et al., 1989). They also conjectured that Brodmann area 45 in the inferior frontal cortex corresponds to a system for representation of grasping movements, functionally similar to F5 in the monkey, where "mirror" neurons were found.

In a third study, cerebral blood flow was measured during observation of actions where both the cognitive strategy of the subjects during the observation and the semantic content of the actions were manipulated (Decety et al., 1997). Subjects were scanned under four conditions of visually presented meaningful or meaningless actions. In each of the four activation conditions, they were instructed to observe actions carefully with one of two aims: to be able to recognise or to imitate them later. The differences in the meaning of actions, irrespective of the strategy used during observation, led to different patterns of brain activity and clear left/right asymmetries. Meaningful actions were associated with activations located in the left hemisphere, in the inferior frontal gyrus (Ba 45), in the middle temporal gyrus (Ba 21), and in the orbitofrontal cortex. This neural network was interpreted to be implicated in the semantic object processing and in action recognition. In contrast, meaningless actions involved mainly the right occipito-parietal pathway, reaching the premotor cortex when the aim of the observation was to imitate. These activations were interpreted to be processing of the visual properties necessary for generating visuomotor transformation, in order to construct a new representation of actions to be imitated. Observing with the intent to recognise activated memory encod-

ing structures, while observing with the intent to imitate was associated with activations located in the dorsolateral prefrontal cortex, the SMA, and the cerebellum. These regions are known to be implicated in the planning and generation of actions (Decety, 1996).

However, an issue that has not fully been considered in these studies is the respective contribution of vision for perception and vision for action. Indeed, in daily life, actions performed by others are usually perceived without any purpose or without requiring further overt integration. On some occasions, however, perception of actions has a specific goal, such as imitation or whenever a decision has to be taken. These considerations raise the interesting question of whether the actions perceived in such a natural context are processed differently according to their nature or meaning (semantic content). A second related interesting issue is to probe whether the aim of the observation has an effect on the visual information processing.

The aim of the present study was to investigate the respective effect of the perception of meaningful and meaningless actions on the neural pathways during nondirected processing that occurs in the absence of explicit instructions as well as when the subject shifts from a passive observation to a more cognitive mode, i.e. the potential contribution of the aim of observation (top-down effect) on the neural network engaged by the nature of the movements. The neural response to the perception of hand action was assessed by measuring regional cerebral blood flow (rCBF) with PET in normal subjects while they observed meaning-

ful or meaningless actions without any purpose and later while they observed similar actions with the aim of imitating them. Finally, to reveal the whole network engaged during the perception of human movements, a control condition with no movements was performed.

## MATERIAL AND METHODS

### Subjects

Ten healthy male volunteers (20–28 years) who had given written informed consent participated in the experiment. All were right-handed according to the Edinburgh Inventory test (Oldfield, 1971) and had normal or corrected-to-normal vision. The experiment was performed in accordance with the guidelines from the declaration of Helsinki and with the approval of the local Ethical Committee (Centre Léon Bérard). Subjects were paid for their participation.

### Activation Tasks

Subjects were scanned 10 times during the observation of video-filmed scenes. Four experimental conditions and one control condition were used according to the instructions given to the subjects (for definition of the five conditions and their abbreviations, see Table 1). Each condition was repeated once and was separated from the next by a 10min inter-scan period. In all activation tasks, video-films consisted of sequences of five actions executed with the upper limbs; these videos showed an

**Table 1.** Five Experimental Conditions

<i>Abbreviation</i>	<i>Nature of the Stimulus</i>	<i>Aim of the Observation</i>
MF	Meaningful action	Without any purpose
ML	Meaningless action	Without any purpose
S	Stationary hands	Without any purpose
IMF	Meaningful action	In order to imitate
IML	Meaningless action	In order to imitate

experimenter's upper limbs and trunk only. Each action, which lasted for 4sec, was separated from the next by a 500msec blank screen. The five actions were presented three times in a random order (15 stimuli per condition). The stimuli were presented in the centre of a colour video monitor (36cm), located in front of the subject at 60cm from their eyes. The screen was oriented so as to be perpendicular to the subject's line of sight. The field of view of the subject was 19° and 26° for the vertical and horizontal dimensions respectively. The video apparatus and the subjects were surrounded by a black curtain. Room lights were reduced to a minimum and cooling fans provided low-level background noise.

In two conditions (MF & IMF), meaningful actions were presented. They consisted of pantomimes of transitive acts (e.g. opening a bottle, drawing a line, sewing a button, hammering a nail) performed by a right-handed person. These actions mainly involved the right (dominant hand); the left was used to hold the represented object. All meaningful actions were gestures that utilise tools with objects or gestures that utilise objects but no tools. Gestures that utilise no tool and no object such those used in communication were excluded.

In two other conditions (ML & IML), meaningless actions were presented. These actions were derived from American Sign Language (ASL), with the constraint that they be perceptually as close as possible to the actions presented during the meaningful actions (e.g. movements involving mainly the right hand). As the subjects had no knowledge of ASL, the actions bore no overt relation to language nor to symbolic gestures.

In one other condition (S), stationary hands were presented. The stimulus structure was the same as that used in activation tasks with the following characteristic: no movements. Five meaningless spatial positions of the hands and limbs were used and randomly presented throughout the condition. The aim of this condition was to provide a reference level for activation tasks, i.e. to subtract the "low-level" visual analysis of the stimuli (upper limb recognition, colour, texture, etc.).

## Experimental Design

The four experimental conditions, duplicated once, were devised in two sessions. In the first, subjects were required to look at video-films without any specific aim. In the second session, subjects were asked to watch the video-films with the aim of imitating the actions presented. The two sessions were performed consecutively using different sets of similar kinds of stimuli.

*First session.* Subjects were instructed to observe carefully meaningful (MF) or meaningless (ML) actions without any specific purpose.

These two conditions (four scans) were presented in a random order in the first session. Subjects were not informed about the nature of the movements presented before the start of the film and thus they were unaware of which category of action would be presented. There was no task performed at the end of the scanning period. Immediately after the end of the PET-data acquisition, subjects were asked to describe what they had seen. Their verbal report were recorded without reinforcement. This question was asked in order to control whether the subjects paid attention to the film and also to see whether they became aware of the nature of the stimuli (i.e. meaningful or meaningless).

*Second session.* Subjects were asked to observe carefully the meaningful (IMF) or meaningless (IML) actions in order to imitate them after the scanning period. These two conditions (four scans) were presented in a random order. Subjects were instructed that they would have to reproduce accurately the five actions that they had seen during the scan. No mention was made concerning the nature of the actions presented. In these conditions, subjects were specifically asked to avoid verbalisation during the observation period (a word couldn't accurately describe a movement) and during the imitation after the scanning period. Immediately after the scanning acquisition, subjects were asked to reproduce the actions presented. The subjects' performance was recorded on a videotape and then scored by an experimenter on a 2-point scale (1 = correctly reproduced, 0 = unrecognisable or not reproduced).

Prior to the first scanning of the second session, and after general instructions had been given, a practice trial composed of five actions was administrated. The video used in the practice trial was different from those during the scanning period.

The control condition (observation of stationary hands) was presented twice and randomly distributed within the two sessions. In this condition (S), subjects were required to observe stationary hands carefully without any specific task.

### Scanning Procedure

Subjects were examined in the supine position on the bed of the PET scanner. Control of the head position throughout the examination was made by laser alignment along with reference points on Reid's line before and after each session. The head was slightly raised above the bed by means of a head holder, which allowed adequate fixation. Subjects could thus look comfortably at the monitor.

PET scans were acquired using a Siemens CTI HR+ (63 slices, 15.2cm axial field of view) PET tomograph with collimating septa retracted operating in high-sensitivity three-dimensional mode. The system has 31 rings which allow acquisition of 63 transaxial images with a slice thickness of 2.42mm without a gap in between. Transmission data were acquired using rotating pin sources filled with  $^{68}\text{Ge}$  (9 mCi/pin). A filtered back-projection algorithm was employed for image reconstruction, on a  $128 \times 128$  matrix (pixel size 2.02mm, Hanning filter with a cut-off fre-

quency of 0.5 cycles/pixel). rCBF was estimated by recording the distribution of radioactivity following the intravenous bolus injection of 333MBq of  $^{15}\text{O}\text{-H}_2\text{O}$  through a forearm cannula placed into the brachial vein. The integrated counts collected for 60sec, starting 20sec after the injection time, were used as an index of rCBF.

At the beginning of the film, specific instructions were given to focus subjects' attention and to tell them what task, if any, was to be performed. The video-film with action sequences was switched on at the same moment as the injection was given. A 10min interval between each condition was necessary for the radioactivity decay.

Each subject also underwent a high-resolution magnetic resonance imaging (MRI) scan (FLASH 3D, T1, 120 slices parallel with the AC-PC plane, 1mm thick) obtained with a Philips 1.5 Tesla magnet.

### Data Analysis

Image analysis was performed on Silicon Graphics O2 stations. The data were analysed with statistical parametric mapping (SPM96 software MRC Cyclotron Unit, London; Friston et al., 1995) implemented in Matlab 4.2 (Math Works, Natick, MA). The structural MRI and the realigned PET images were spatially normalised into a standard stereotaxic space (Talairach & Tournoux, 1988) using a reference template image (Friston et al., 1995). The resulting voxel dimensions of each reconstructed scan was  $2 \times 2 \times 4\text{mm}$  in the x, y, and z dimension, respectively. The scan were

smoothed using a gaussian filter of 12mm full width at half-maximum. Global differences in cerebral blood flow were covaried out for all voxels and comparisons across conditions were made using *t* statistics with appropriate linear contrasts, and then converted to Z scores. Only regional activations significant at  $P < .001$  uncorrected for multiple comparisons ( $Z > 3.09$ ) were considered. In addition to this standard procedure, and in order to improve the precise anatomical description, the activation foci were superimposed both on a reference MRI from one normal subject, available in SMP96, and on the averaged MRI from the 10 study subjects. Since the comparison between the individual MRI and the averaged MRI was in good correspondence (for the overlapping of the major sulci), we decided to use the individual MRI in order to localise peak sites. Anatomical identification was performed with reference to the atlas of Talairach and Tournoux (1988) as well as the atlas of Duvernoy (1991).

### Statistical Analysis

The differences between conditions were assessed by comparisons of specific rCBF maps pertaining to the experimental conditions.

### Simple Main Effects

The subtractions of the control condition (S) from the observation without any purpose of meaningful actions (MF-S) and of meaningless actions (ML-S) were performed in order to reveal the whole network engaged by the perception of human movements and also to de-

termine whether meaningful and meaningless actions are processed differently.

The subtractions of the control condition (S) from observation to imitation of meaningful actions (IMF-S) and of meaningless actions (IML-S) allowed the determination of whether the strategy to imitate has an effect on the neural network involved by the perception of actions.

### Main Effect

In order to isolate the network engaged by the strategy to imitate during the observation of actions, irrespective of the nature of the actions presented, a factorial subtraction was computed according to the formula: [(IMF + IML) - (MF + ML)].

### Task-related Regional Activity

Post hoc analysis, which is a descriptive analysis and not a quantitative one, was occasionally performed, using the stereotactic coordinates of some relevant activation foci found in the categorical comparisons. These profiles of activity, which represent relative rCBF values in each task, were used to demonstrate the differential involvement of a selected brain area in the five experimental conditions.

## RESULTS

### Subjects' Performances

The subjects achieved 89% correct in the imitation of meaningful actions, and 80% in the imitation of meaningless actions.

## PET Results

The results from simple main effect relative to comparisons between experimental conditions and the control condition will first be presented. Then, the main effect relative to the strategy used during the observation (to imitate), irrespective of the nature of the movements will be presented.

### **Simple Main Effect Related to the Observation of Actions (Meaningful or Meaningless) Relative to the Observation of Stationary Hands**

See Tables 2 and 3.

*Observation of meaningful movements (MF-S).* Observing meaningful movements without any purpose versus stationary hands was associated with activations in the superior occipital gyrus (Ba 19) and in the occipital

temporal junction (Ba 19/37) bilaterally. Significant activation was found in the left inferior frontal gyrus, with the peak located in the fundus of the sulcus between Ba 44 and Ba 45. The precentral gyrus (Ba 4), the middle temporal gyrus (Ba 21), and the inferior parietal lobe in its ventrorostral part (Ba 40) were activated in the left hemisphere, whereas the lingual gyrus (19/18) and the superior temporal gyrus were activated in the right hemisphere. rCBF increases were also found in the fusiform gyrus (Ba 20) and in the inferior temporal gyrus (Ba 20/38) in the left hemisphere (Fig. 1). Post hoc exploration, which was a qualitative analysis, performed for the peak site located in the left inferior frontal gyrus (Ba 44/45) showed that this region was predominantly involved during the observation of meaningful actions without any purpose and much less during the other activation conditions (Fig. 2).

**Table 2.** Cortical Foci (Local Maxima) Demonstrating Significant rCBF Increases During Observation of Meaningful Actions vs. Observation of Stationary Hands

Brain Region	L/R	Brodmann Area	Coordinates			Z Score
			x	y	z	
Precentral gyrus	L	4	-34	-12	48	3.95
Superior occipital gyrus	R	19	24	-86	36	4.15
Superior occipital gyrus	L	19	-28	-86	30	3.91
Inferior parietal lobe ventrorostral	L	40	-64	-26	24	4.75
Inferior frontal gyrus	L	44/45	-48	12	22	3.65
Superior temporal gyrus	R	22	64	-38	16	5.23
Middle temporal gyrus	L	21	-60	-46	10	4.59
Occipital temporal junction	L	37/19	-46	-64	6	5.29
Gyrus lingual inferior	R	19/18	8	-64	0	4.06
Occipital temporal junction	R	37/19	44	-64	0	5.79
Fusiform gyrus	L	20	-50	-46	-24	3.53
Inferior temporal gyrus	L	20/38	-34	-4	-36	4.40

Coordinates are in mm and correspond to the Talairach and Tournoux atlas (1988). L/R: left or right hemisphere. Threshold = 3.09 ( $P < .001$ ).

**Table 3.** Cortical Foci (Local Maxima) Demonstrating Significant rCBF Increases During Observation of Meaningless Actions vs. Observation of Stationary Hands

Brain Region	L/R	Brodmann Area	Coordinates			Z Score
			x	y	z	
Superior parietal lobule	L	7	-26	-54	70	4.16
Superior parietal lobule	L	7/40	-34	-44	66	5.41
Superior parietal lobule	R	7	32	-46	62	4.19
Precentral gyrus	L	4	-34	-12	48	2.95*
Inferior parietal lobe	R	40	40	-38	46	5.46
Superior occipital gyrus	R	19	24	-84	36	5.60
Superior occipital gyrus	L	19	-18	-88	32	3.62
Inferior parietal lobe ventrorostral	L	40	-62	-28	24	5.69
Superior temporal gyrus	R	22	68	-38	18	6.65
Middle temporal gyrus	L	21	-58	-50	10	3.36
Occipital temporal junction	L	37/19	-46	-64	6	5.94
Occipital temporal junction	R	37/19	44	-62	0	6.70
Cerebellum	R		26	-48	-46	3.67

\*  $P < .01$   $Z = 2.33$ .

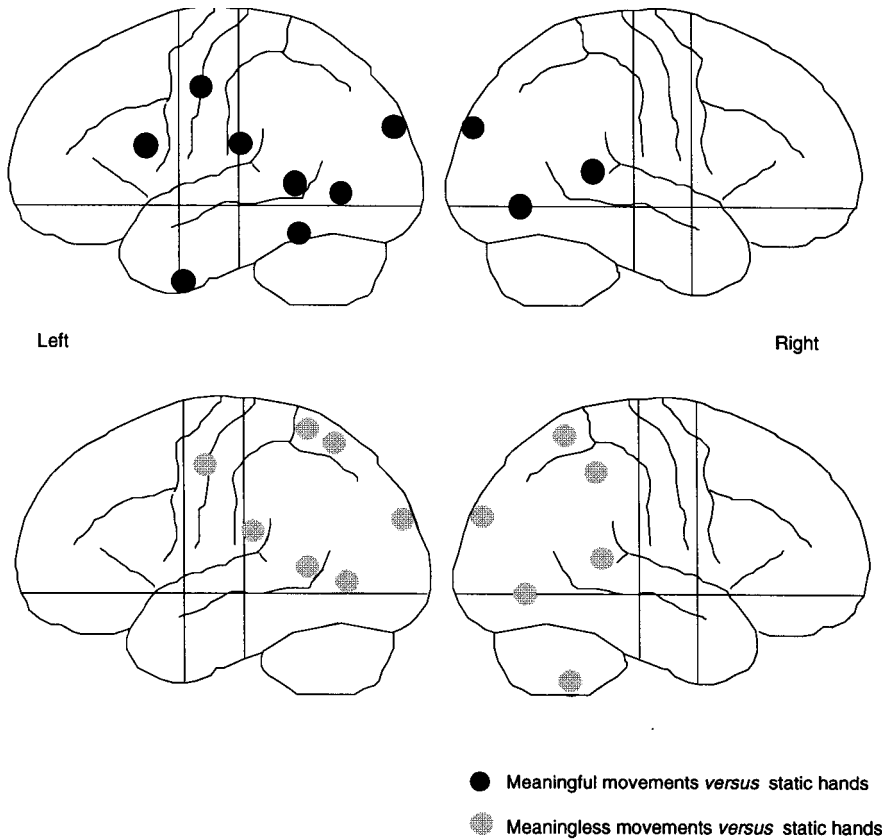
*Observation of meaningless movements (ML-S).* Activations produced by the observation of meaningless actions without any purpose, as contrasted to stationary hands, were located bilaterally in the superior occipital gyrus (Ba 19) and the occipital temporal junction (Ba 19/37). A large and strong activation was found in the right parietal lobe, whose area covered the superior parietal lobule (Ba 7) following the intraparietal sulcus and extending into the inferior parietal lobe in its upper portion (Ba 40). On the left side, a similar activation was found, but it was weaker and less extensive. This activation spread throughout the superior parietal lobule (Ba 7) and followed the intraparietal sulcus up to its most anterior part. An independent focus of rCBF increase was also located in the left inferior parietal lobe in its ventrorostral part (Ba 40). Activations were also found in the precentral gyrus (Ba 4),

in the middle temporal gyrus (Ba 21) in the left hemisphere and in the superior temporal gyrus (Ba 22) and in the cerebellum on the right side (Fig. 1).

#### **Simple Main Effect Related to the Observation of Actions (Meaningful or Meaningless) in Order to Imitate vs. Stationary Hands**

See Tables 4 and 5.

*Observation of meaningful actions to imitate (IMF-S).* Most of the rCBF increases during observation of meaningful actions to imitate versus stationary hands, were located in both hemispheres. The occipital temporal junction (Ba 19/37), the SMA (mesial Ba 6) and the middle frontal gyrus (fundus of Ba 6) were found to be activated. In addition, the superior parietal lobule (Ba 7) extending into the upper part of the intraparietal sulcus (between the

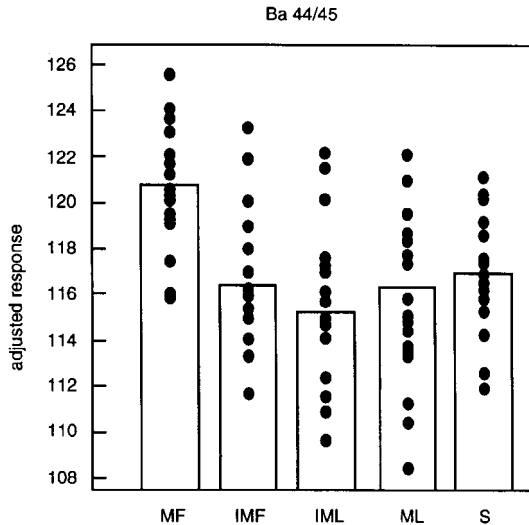


**Fig. 1.** Lateral view of the left and right hemispheres showing cortical regions of increased rCBF during observation of meaningful and meaningless actions without any purpose, compared to the observation of stationary hands. Results are listed in Tables 2 and 3.

coordinates  $y = -54$  to  $y = -30$ , Ba 7/40) and the inferior parietal lobe in its upper part (Ba 40) were found to be activated. Although the centre of gravity of these activations are similar the two hemispheres, the areas belonging to them were broader in the left hemisphere. The inferior parietal lobe in its ventrorostral part (Ba 40) was activated in the left hemisphere. This latter focus was independent of the other foci in the parietal cortex. In the right hemisphere, the superior occipital gyrus (Ba 19), the

superior temporal gyrus (Ba 22), and the cerebellum appeared to be involved. Bilateral activations were also found in the orbital gyrus (Ba 11) (Fig. 3).

*Observation of meaningless actions to imitate (IML-S).* During observation of meaningless actions to imitate versus stationary hands, activations were located in the middle frontal gyrus (fundus of Ba 6), in the occipital temporal junction (Ba 19/37), and in the cerebellum



**Fig. 2.** Results of the post hoc exploration performed from a voxel (local maxima) in the inferior frontal gyrus (Brodmann's areas 44/45:  $x = -48$ ,  $y = 12$ ,  $z = 22$ ). The profile of activity illustrates relative rCBF value in each experimental conditions. The black circles represent the distribution of each scan for the 10 subjects in each experimental condition. Note the prevalent involvement of this region during the observation of meaningful actions without any purpose (MF).

in both hemispheres. Bilateral and comparable activations were found in the parietal cortex, although they were stronger in the left hemisphere. These activations spread out from the superior occipital gyrus (Ba 19) to the superior parietal lobule (Ba 7) extending into the upper section of the intraparietal sulcus (Ba 7/40). Activations were found in the right hemisphere in the superior temporal gyrus (Ba 22) and in the inferior parietal lobe in its upper part (Ba 40). The ventral part of the precentral gyrus (Ba 6) and the inferior parietal lobe in its ventrorostral part (Ba 40) were also activated in the left hemisphere (Fig. 3).

### **Main Effect Due to the Strategy to Imitate During Observation of Actions vs. Observation without Any Purpose $\{(IMF + IML) - (MF + ML)\}$**

See Table 6. Observation in order to imitate versus observation without any purpose, irrespective of the nature of the stimuli, was associated with activations located bilaterally in the middle frontal gyrus (Ba 9), in the premotor cortex (Ba 6) and in the SMA. The inferior parietal gyrus (Ba 40), in its upper section, the superior parietal lobule (Ba 7), and the anterior cingulate gyrus (Ba 32) were activated on both sides. At the subcortical level, the medio-dorsal thalamic nucleus was found to be activated in the right hemisphere, whereas the posterior caudate nucleus was activated in both sides. The dorsal frontal gyrus (Ba 10), the cerebellum, and the cuneus (Ba 17/18) were activated in both hemispheres. rCBF increases were also found in the precuneus (Ba 7) and in the middle frontal gyrus (Ba 46) in the left hemisphere (Fig. 4).

Post hoc exploration performed for the activation located in the middle frontal gyrus (Ba 9) showed that this region was involved both during observation to imitate (IMF and IML) and during the control condition (stationary hands S) (Fig. 5).

## **DISCUSSION**

### **Perception of Human Movements**

The subtractions of the baseline condition (stationary hands) from the four target conditions

**Table 4.** Cortical Foci (Local Maxima) Demonstrating Significant rCBF Increases During Observation of Meaningful Actions in Order to Imitate vs. Stationary Hands

Brain Region	L/R	Brodmann Area	Coordinates			Z Score
			x	y	z	
Intraparietal sulcus	R	7/40	44	-42	64	4.80
Superior parietal lobule	L	7	-18	-70	64	4.73
Mesial frontal gyrus (SMA)	L	6	-6	-4	60	3.44
Intraparietal sulcus	L	7/40	-44	-46	58	4.12
Middle frontal gyrus (fundus)	L	6	-26	-6	56	3.75
Superior parietal lobule	R	7	24	-62	54	3.40
Middle frontal gyrus (fundus)	R	6	32	-6	52	3.77
Mesial frontal gyrus (SMA) anterior	R	6	2	8	52	3.32
Inferior parietal lobe	R	40	40	-38	44	5.40
Inferior parietal lobe	L	40	-58	-32	40	3.94
Superior occipital gyrus	R	19	22	-86	36	5.63
Inferior parietal lobe ventrorostral	L	40	-66	-26	26	4.34
Superior temporal gyrus	R	22	72	-36	16	4.73
Occipital temporal junction	L	37/19	-50	-68	2	4.69
Occipital temporal junction	R	37/19	46	-60	0	6.82
Orbital gyrus	L	11	-22	36	-30	3.69
Orbital gyrus	R	11	28	30	-30	3.68
Cerebellum	R		28	-48	-44	5.39

showed that several cortical areas were involved regardless of either the semantic content of the movements or the purpose of the observation. It is thus natural to interpret these activations as reflecting hand movement analysis.

The activation of the occipito-temporal junction (Ba 19/37) corresponds precisely to the coordinates of V5 given by Watson et al. (1993) from a PET study in humans. This region is known to be specifically engaged by visual motion and would be the homologue of the middle temporal area (MT) in monkey. Vaina, Lemay, Bienfang, Choi, and Nakayama (1990) reported a related case of a patient with bilateral lesions involving the temporal-parie-

tal-occipital junction, presumably damaging the human homologue of MT, sparing the primary visual cortex. This patient was severely impaired on motion tasks but was normal on higher-order tasks, exhibiting no deficits in the Johansson biological motion tasks. Another single-case study, reported by Marcar, Zihl, and Cowey (1997), came to the same conclusion. These findings imply that V5 is not essential for processing biological motion and/or that there is a separate motion pathway specialised for the perception of biological motion (as suggested by Colby, Gattas, Olson, & Gross 1988). Other activations, which pertain to the dorsal stream and are located in the superior occipital gyrus (Ba 19) and in the

**Table 5.** Cortical Foci (Local Maxima) Demonstrating Significant rCBF Increases During Observation of Meaningless Actions in Order to Imitate vs. Stationary Hands

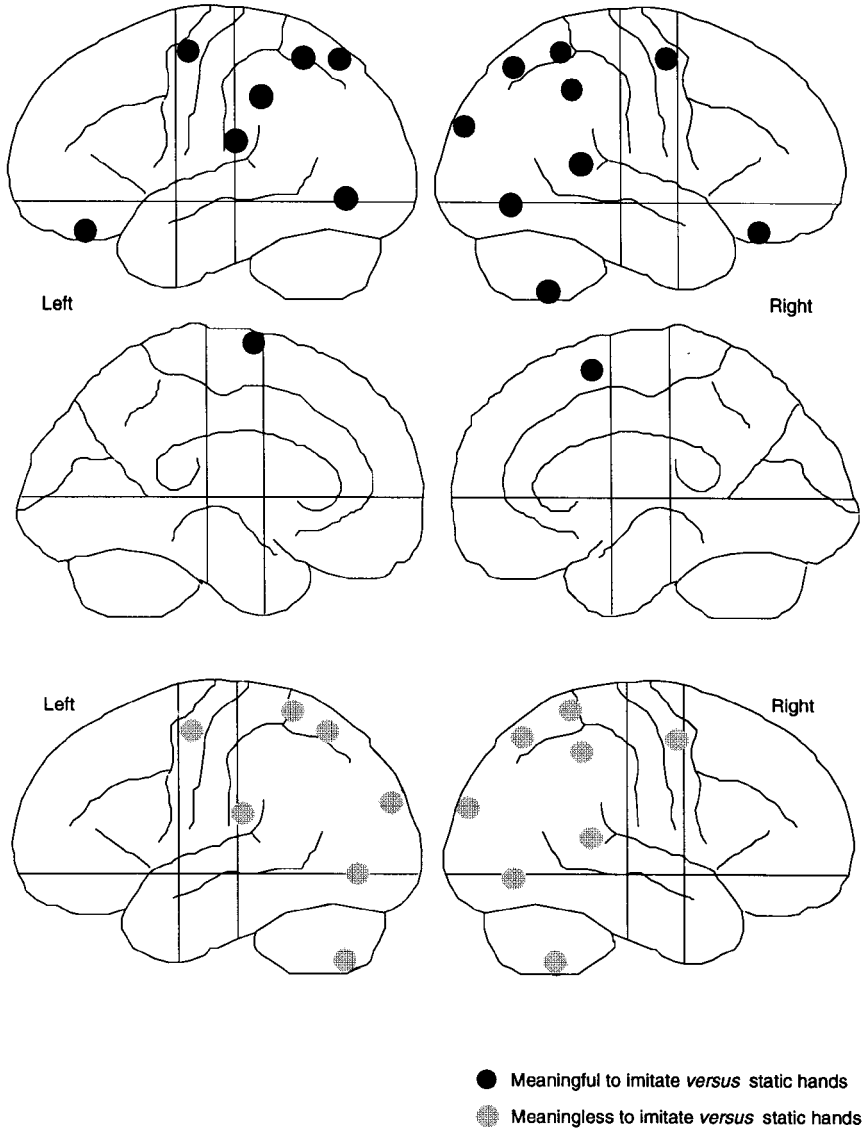
Brain Region	L/R	Brodmann Area	Coordinates			Z Score
			x	y	z	
Intraparietal sulcus	L	7/40	-34	-44	64	4.89
Intraparietal sulcus	R	7/40	44	-42	62	3.50
Superior parietal lobule	L	7	-24	-60	62	6.41
Middle frontal gyrus (fundus)	L	6	-26	-6	56	3.75
Superior parietal lobule	R	7	24	-66	54	4.85
Middle frontal gyrus (fundus)	R	6	32	-8	50	3.86
Inferior parietal lobe	R	40	40	-40	46	5.15
Superior occipital gyrus	L	19	-20	-84	40	4.77
Superior occipital gyrus	R	19	26	-84	36	4.82
Inferior parietal lobe ventrorostral	L	40	-64	-26	28	4.50
Superior temporal gyrus	R	22	66	-38	18	4.18
Occipital temporal junction	L	37/19	-48	-70	0	5.74
Occipital temporal junction	R	37/19	44	-64	0	6.19
Cerebellum	L		-36	-50	-34	3.99
Cerebellum	R		34	-42	-42	5.41

parietal lobe, may be related to the spatial analysis of hand actions and knowledge of body in space (Kupfermann, 1991).

### Perception of Actions without Any Purpose: Effect of the Meaning

The activation in the rostral part of Brodmann's area 21 in the left hemisphere was found during the observation of meaningful and meaningless actions without a goal. The fact that this region was activated during perception of meaningless actions is rather surprising since it is often claimed that this region is specifically involved in purposeful actions.

The left primary motor cortex was found to be activated during perception of meaningful and meaningless movements without any purpose. This activation, which is precisely located within the representation of hand area, in the contralateral hemisphere was also found to be activated in actual motor tasks (Matelli et al., 1993) as well as in motor imagery of hand movement (Parsons et al., 1995; Porro et al., 1996; Roth et al., 1996). Such activation is a good argument in favour of the motor theory of perception, which postulates that intrinsic properties of the motor control system may interact with visual perception of actions. It is, to our knowledge, the first and most direct demonstration of the involvement of the primary motor cortex during the perception of hand actions.



**Fig. 3.** Localisation of activated foci during observation of meaningful and meaningless actions, with the intent to imitate, compared to the observation of stationary hands. Lateral views are shown on the top, and medial views on the bottom for meaningful actions, and only lateral views are provided for meaningless actions. Results are listed in Tables 4 and 5.

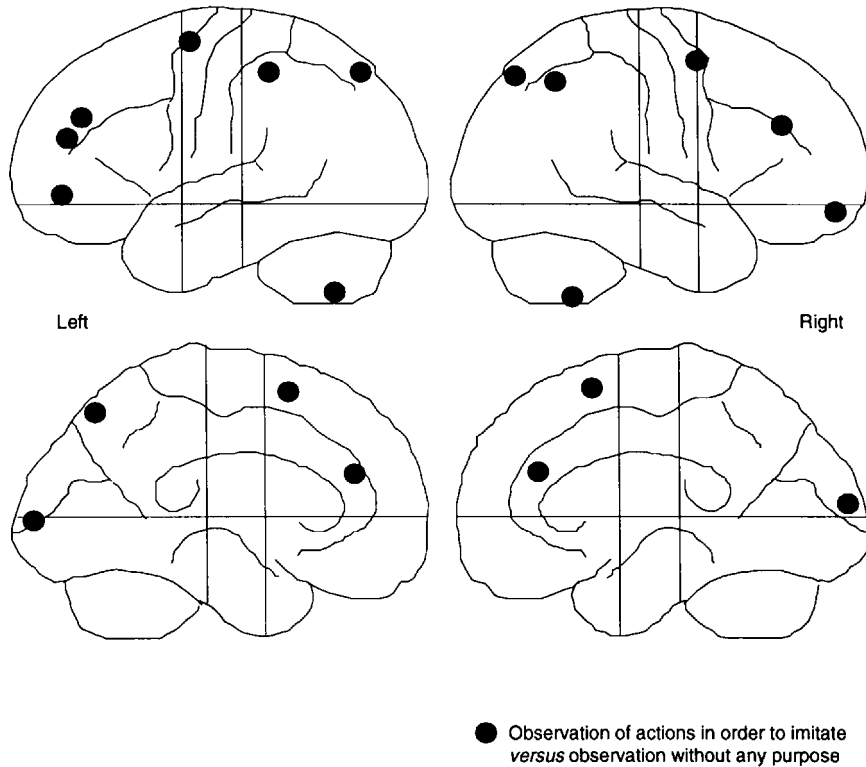
**Table 6.** Cortical Foci (Local Maxima) Demonstrating Significant rCBF Increases During Observation of Actions in Order to Imitate v. Observation without Any Purpose, Irrespective of the Nature of the Movements (IMF + IML) - (MF + ML)

Brain Region	L/R	Brodmann Area	Coordinates			Z Score
			x	y	z	
Superior frontal gyrus (fundus)	L	6	-24	-6	64	4.72
Precuneus	L	7	-8	-72	60	5.93
Superior parietal lobule	L	7	-20	-70	62	5.13
Superior parietal lobule	R	7	18	-70	56	5.32
Middle frontal gyrus	R	6	28	2	56	4.51
Inferior parietal lobe	R	40	56	-52	50	4.40
Inferior parietal lobe	L	40	-48	-34	50	4.25
Mesial frontal gyrus (SMA) anterior	R	6	2	10	50	3.36
Mesial frontal gyrus (SMA)	L	6	-6	10	46	3.46
Middle frontal gyrus	L	9	-38	32	34	5.41
Middle frontal gyrus	R	9	28	32	32	4.55
Middle frontal gyrus	L	46	-44	36	28	5.21
Caudate nucleus posterior	L		-20	-30	24	4.55
Caudate nucleus posterior	R		12	-14	22	3.77
Cingulate gyrus	L	32	-18	34	22	4.00
Cingulate gyrus	R	32	24	32	20	4.44
Dorsal medial nucleus of the thalamus	R		4	-22	10	4.07
Dorsal frontal gyrus	L	10	-18	-44	6	3.60
Cuneus	R	17/19	4	-104	4	5.21
Dorsal frontal gyrus	R	10	28	50	-2	3.60
Cuneus	L	17/18	-14	-104	-2	4.63
Cerebellum	R		36	-44	-40	5.32
Cerebellum	L		-34	-54	-36	5.17

### Meaningful Actions

In addition to this common network involved in all activation conditions, observation of meaningful and meaningless actions without any aim engaged specific brain regions respectively. Meaningful actions activated the inferior frontal gyrus (Ba 44/45) and the fusiform gyrus (Ba 37/38) in the left hemisphere. On the right side, the inferior temporal gyrus (Ba 19/18) was activated. Meaningful and meaningless actions only differed in terms of semantic content and were constructed in order to be

as close as possible in their physical properties. It is thus possible that subjects may have decoded pantomimes in order to identify which objects are involved in each action presented. Activations located in the ventral pathway, corresponding to the fusiform and to the anterior part of the inferior temporal gyrus, are coherent with the hierarchical organisation of the ventral occipito-temporal pathway proposed by Ungerleider (1995), in the sense that low-level inputs (visual features of stimuli) are transformed into progressively more useful

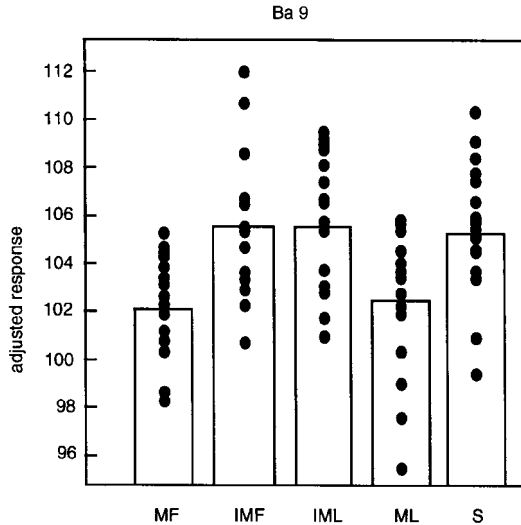


**Fig. 4.** Lateral (top) and medial (bottom) views of the left and right hemispheres showing cortical regions of increased rCBF during observation of actions in order to imitate, compared to the observation without any purpose, and irrespective of the nature of the stimuli. Results are listed in Table 6.

representations (semantic) through successive stages of processing.

Thus, observation of pantomimes activated a neural network in the left hemisphere that may be related to the semantic aspects of knowledge that are decoded from the visual patterns of motion associated with object use (temporal areas and fusiform) and also with their associated motor commands (precentral gyrus). This activation condition may also be considered as an implicit recognition task. In-

deed, in our previous study, observation of meaningful actions with the purpose of recognition (i.e. an explicit recognition task) led to comparable activations in the inferior frontal gyrus and in the inferior temporal gyrus (Decety et al., 1997). The only differences in term of activated areas between the two studies were the involvement of the parahippocampal gyrus and of the middle temporal gyrus, found in the first study. The absence of activation in the parahippocampal gyrus may be inter-



**Fig. 5.** Results of post hoc exploration performed from a voxel (local maxima) in the middle frontal gyrus (Brodmann area 9:  $x = -38$ ,  $y = 32$ ,  $z = 34$ ). The profile of activity illustrates relative rCBF value in each experimental condition. The black circles represent the distribution of each scan for the 10 subjects in each experimental condition. Note that this region is heavily involved during the condition of observation that required to imitate (IMF and IML), and similarly during the control condition (S).

preted by the difference in task demand, since no working memory component was necessary this time.

Concerning the activation located in the left inferior frontal gyrus at the border between Ba 44 and 45, post hoc analysis indicated that this region was essentially implicated in the observation of meaningful actions without any purpose. Brodmann's areas 44 and 45 (Broca's area in the left hemisphere) might correspond to the ventral premotor cortex in the macaque (Matelli & Luppino, 1997; Petrides & Pandya, 1994). This activation may be interpreted as

reflecting its involvement in action recognition as suggested by Rizzolatti et al. (1996). This result, reported here, is in agreement with Decety et al. (1997), who found activation in the left inferior frontal gyrus during observation of meaningful action with the strategy to recognise them later. However, the lack of activation of this region during observation to imitate is, to some extent, in contradiction with the Rizzolatti et al. (1996) interpretation, namely the area is engaged both during observation and execution, homologous to part of F5 in the macaque. Such a matching system is not yet demonstrated in man since Brodmann's areas 44 and 45 were not found activated during execution of grasping but only during observation. This activation may also be interpreted as reflecting either silent speech processing or the access to semantic knowledge of action as proposed by Perani et al. (1995) from a PET-activation study on recognition of tools.

### Meaningless Actions

Meaningless actions were associated with activations located in the superior parietal lobule (Ba 7), in the inferior parietal lobe in its upper part (Ba 40) in both hemispheres, and in the cerebellum in the right hemisphere. These results support the PET findings from the previous experiment (Decety et al., 1997). However, the activation of the dorsal pathway is now bilateral, and not restricted to the right hemisphere as in the first study. This is probably due to the control condition (stationary hands), which was subtracted from this condition. The activation of the occipito-parietal

pathway is coherent with the role of the dorsal pathway for processing visual properties of the bodily movements and for generating visuomotor transformations. Lesions in the superior parietal lobule produce subtle deficits in purposive and skilful behaviour of the hand (Andersen & Zipser, 1988). The fact that meaningless and unfamiliar actions can only be decoded in terms of their spatiotemporal layout, which includes direction of movements in 3-D space and kinematics, is consistent with a predominant activation of the dorsal pathway.

### **Influence of the Strategy on Action Perception**

Perception of meaningful and meaningless actions with the aim to reproduce them later engaged a rather similar network, although the activations were stronger for meaningless actions. Activations were mainly located in the dorsal pathway extending to the premotor cortex in both hemispheres. Specific bilateral activations for meaningful actions were found in the SMA and in the orbital gyrus. This result is coherent with the division of labour within the visual system that considers a clear distinction between the ventral stream involved in recognition, and the dorsal pathway involved in action (Milner & Goodale, 1995). Among several functions subserved by the visuomotor network in the dorsal stream and associated cortical and subcortical regions are viewer-centred visuomotor transformations used in action planning. It is the nature of the requirement of perception (action/perception) that determines which pathway would be engaged (Goodale, 1997; Goodale & Milner, 1992; Mil-

ner & Goodale, 1995). Remarkable dissociations have been observed in patients with visual agnosia following temporal lesions who were found to be able to perform object-oriented action without being capable of identifying objects, and the reverse in patients with parietal lesions (Goodale, Milner, Jakobson, & Carey, 1991; Jeannerod, Decety, & Michel, 1994; Sirigu et al., 1995; Sirigu, Grafman, Bressler, & Sunderland, 1991). These dissociations indicate that the appropriate representation for the use of objects can be elaborated and can operate independently of the temporal cortex. Therefore, vision for action does not necessitate access to semantic knowledge of objects. This conclusion may account for the brain activations found during perception of pantomimes to imitate.

It can be acknowledged that in the intact brain, the two pathways work together in the planning and execution of a goal-directed action. Goal selection requires object recognition as well as semantic information about objects. Both play a role in the control of hand posture when reaching and grasping, for instance (Jeannerod & Decety, 1990). On the basis of a recent study on perception of biological motion, Dittrich (1993) proposed that the process of action coding may involve not only structural components based on the similarity of movements but also semantic coding occurring at very early stages of movement information processing, and that these two types of coding are not separated. Dittrich further argued that this type of action coding is important not only in representing actions but also in perceiving biological motion. On this basis,

one could predict that the perception of meaningful actions to imitate would engage the ventral stream in order to identify and recognise the actions observed, whereas meaningless actions, which are unknown and thus impossible to recognise, would only involve the dorsal stream. Yet our results are, to some extent, in contradiction with this hypothesis. Indeed, observation of meaningful and meaningless actions in order to imitate them later were associated with activations located only in the dorsal stream without any participation of the ventral stream. It can be argued that the lack of activation of the ventral stream is due to the fact that our meaningful actions are pantomimes with represented objects, and that the ventral stream would have been activated if meaningful actions involved the utilisation of real objects. Nevertheless, the ventral stream was found to be engaged during the perception of meaningful actions without any purpose as well as during the observation with the aim to recognise in a previous PET-activation study (Decety et al., 1997). It is also conceivable that the design of the experiment in two sessions has influenced the processing of the nature of the stimuli, through a habituation effect, which led in the second session to a pre-eminent involvement of the dorsal pathway.

Thus, it appears that the reproduction of action that involves initial observation, does not require the semantic integration or verbal labelling. Such a result is not so inconsistent with experiments in the field of observational learning that have shown that a facilitatory effect is measured only after eight opportuni-

ties to observe the modelled actions (Carroll & Bandura, 1990). In the present experiment, the actions were presented three times. Thus, verbal labelling is no help for reproduction if the movements are observed a few times.

From accumulated findings in clinical neuropsychology on apraxic patients, we could have expected a more clear difference between meaningful and meaningless actions when the intention is to imitate observed actions. To account for the dissociation between meaningful and meaningless, Rothi et al. (1991) proposed a cognitive model that postulates two routes: a lexical (semantic) route and a direct, nonlexical one, which respectively mediate vision and motor control in imitation of actions. The lexical route is composed by long-term memory representations of meaningful and familiar actions. The other route provides a direct link between visual analysis of gestures and motor control. This latter one can be used for imitation of both meaningless and meaningful actions. According to this model, when the lexical route is interrupted, imitation of meaningful and meaningless actions is preserved, yet patients are impaired in action recognition. In contrast, the interruption of the direct route gives rise to the dissociation between impaired imitation of meaningless gestures and preserves performance of meaningful actions. Our results show that observation of meaningful actions without any purpose involved the lexical (semantic) route, whereas observation of meaningful and meaningless actions with the aim to imitate them later engaged only the direct route. This finding is consistent with the discrepancy between

gesture comprehension and imitation found in some apraxic patients (Rothi et al., 1986). It is also coherent with the distinction proposed by Milner and Goodale (1995), if one draws a parallel between the lexical route and the ventral pathway and between the direct route and the dorsal pathway. In this case, then, the lexical route is engaged during vision for perception or comprehension, and the direct route is involved during vision for action as well as vision for imitation.

The hypothesis that perception of actions can be directly linked to generative (i.e. motor) processes is supported by several studies. Berger, Carli, Hammersla, Karshmer, and Sanchez (1979) demonstrated by electromyography that observation of body movements is associated with specific innervation in the corresponding muscles. Later, Fadiga, Fogassi, Pavesi, and Rizzolatti (1995) confirmed this result, by applying transcranial magnetic stimulation to subjects' motor cortex during observation of grasping movements without any purpose of imitating them. The results showed that there were an increase in motor evoked potential, recorded from hand muscles, during movement perception. These experiments support the notion of a direct link between perception and action. However, they do not explain how this route translates visual information into motor commands. Goldenberg and Hagmann (1997) recently suggested that imitation of meaningless gestures involves an intermediate step that allows elaboration of a mental representation of the gestures. The fact that cortical areas involved in motor planning are found to be activated

during the observation of meaningless actions, when the intention is to imitate later, speaks in favour of an elaboration of motor representations held in working memory.

Observation of meaningless actions in order to imitate them was associated with bilateral rCBF increases in the dorsal stream extending into the dorsal lateral premotor cortex. This latter region is known to be implicated in action planning and externally triggered action (Passingham, 1993) and is connected with the superior parietal lobule (Jackson & Husain, 1996). Thus, this network is used to integrate the actions perceived with the goal to be reproduced. Activations elicited by the observation of meaningful actions in order to imitate them were located in the same regions but additional increases were found in the SMA, in the orbitofrontal cortex, and in the left inferior parietal lobule. Meaningful actions rely on mental representation in long-term memory. The activation of the SMA is coherent with this hypothesis. Indeed, this region is known to participate in the programming and planning of internally guided actions (Passingham, 1996; Tanji & Shima, 1994). This activation is also consistent with the interpretation given by Watson, Fleet, Rothi, and Heilman (1986) concerning its involvement in transitive limb movements. The fact that the primary motor cortex was not found activated when the purpose of the observation was to imitate may sound puzzling. Our interpretation is that, since the task was to reproduce a sequence of five actions, subjects were engaged in action planning at a higher level which didn't require coding of specific motor commands for each

action. It could be speculated that if the observation applied only one action and not a sequence, then the primary motor cortex may have been implicated.

The activation located in the orbitofrontal cortex has also been found in the Decety et al. (1997) study. This region may play a role in the inhibition of actions which have to be imitated later. Lhermitte, Pillon, and Serdaru (1986) observed patients with lesions in this part of the frontal cortex who exhibit an exaggerated dependence on environmental cues (imitation behaviour or utilisation behaviour). The authors interpreted these behaviours as a consequence of impaired inhibition on the parietal cortex of automatic actions. Other evidence in support of the inhibitory role of the orbitofrontal cortex has recently been reported by Marshall, Halligan, Fink, Wade, and Frackowiak (1997) from a PET-activation study in a single case of left-sided hysterical paralysis. When asked to attempt to move her paralysed leg, the right orbito-frontal cortex was significantly activated.

### **Observation of Actions with the Intent to Imitate**

The effect of the strategy to imitate, as such (i.e. irrespective of the nature of the stimuli), was associated with activations in several cortical areas (SMA, premotor cortex, prefrontal cortex, anterior cingulate), subcortical nuclei (caudate and thalamus), and in the cerebellum. These regions are similar to those found in several neurophysiological studies during motor preparation tasks as well as

during mental simulation of action (Decety et al., 1992, 1994; Stephan et al., 1995). They are usually interpreted as implicating motor representations (Crammond, 1997; Decety, 1996) and, in our study, they implicate motor representations during the stage of observation.

The involvement of the middle frontal gyrus (Ba 9) found in the factorial subtraction disappears when the control condition is subtracted from the target conditions. This could be explained (based on post hoc analysis) by the fact that this region was also involved in observation of stationary hands. According to Shiffrar and Freyd (1993), during the perception of realistic photographs of a human body in different positions, the visual system constructs paths of apparent motion that are consistent with the biomechanical limitations of human body. The perception of different stationary hand positions may have led to such process, although the presentation of each position lasted 4 seconds (which is much longer than the paradigm of Shiffrar & Freyd, 1993). Thus, it cannot be excluded that there is an involvement of the middle frontal cortex in order to keep in mind the stationary position and imagine covertly the movements between two stationary hand positions.

### **CONCLUSION**

Perception of human biological motion led to specific activations depending on the nature of the actions presented when subjects were

given no instructed purpose. The activated regions during the observation of meaningful actions lead us to propose that not only fine visual analysis of hand motion takes place but also the semantic integration of their meaning. It can also be proposed that actions are implicitly decoded in terms of motor production. This hypothesis is consistent with motor theories of perception, and it seems to be true for both meaningful and meaningless actions. The latter additionally necessitate a visuospatial analysis of the hand moving in space.

The perceptual system is conceived as being cognitively impenetrable (Fodor & Pylyshyn, 1981). In addition, the direct theory of perception posits that sensory information from behavioural events are organised by an autonomous perceptual system in which inferences, attitudes, and other cognitive influences do not play a major role. To what extent is perception of biological motion encapsulated? We have seen that a common network was activated by the perception of meaningful and meaningless actions, both of which are biological motion. This network may be a cognitive encapsulated part of the perceptual analysis. The specific activations relative to the nature of the biological stimuli, and most notably the influence of the strategy to imitate, clearly demonstrate that there is a modulatory effect on the neural network during the perception phase.

Indeed, when the observation has a goal, namely the intention to imitate, it appears that there is much less specificity of the neural networks involved, relative to the nature of the stimulus. The activations in the ventral path-

way are no longer observed when observation of meaningful actions has a goal (to imitate). Only the dorsal pathway was strongly activated, reaching the lateral and the mesial premotor cortex. The same picture holds true for meaningless action and the intention to imitate, with the exception of the mesial premotor cortex. There is thus a clear top-down effect of the strategy (to imitate) upon the information processing, at least in terms of activated regions. These results further demonstrate the pre-eminent role of the dorsal pathway in perception for action, as suggested by Milner and Goodale (1995).

Some of these results are surprising in light of the literature on apraxia (e.g. Heilman et al., 1982; Heilman, Watson, & Rothi, 1997), in which most of the clinical observations have pointed to a role of the supramarginal and angular gyri in movement comprehension and imitation. These two regions were not found to be activated in our study and there are several possible reasons to account for this discrepancy. First, our experimental paradigm was designed to identify the regions engaged during the perception phase which was, in some conditions, followed by imitation. This condition corresponds to deferred imitation and not to immediate imitation as it is often studied in patients. Thus, the differences within the posterior parietal cortex may be explained in terms of task requirement. Indeed, deferred imitation necessitates temporary stored action planning, whereas immediate imitation engages on-line control. These two processes are known to rely on different neural networks. Second, lesion sites can vary in accuracy and

location across patients; it is best if the lesions are stable, well demarcated, and referable to a neuroanatomic unit. Finally, our findings are based on group data (i.e. averaged images). All of these remarks may explain the partial overlap between the two sets of data (normal subjects/patients). This overlap illustrates why it is useful to combine empirical work on apraxia with studies performed on normal subjects and neurophysiological recordings to elucidate the neural and cognitive mechanisms involved in the perception, the recognition, and the generation of actions. This also affirmatively answers the provocative question that is often raised as to whether PET is a method capable of generating and testing new hypotheses or merely of confirming old ones.

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