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Brain activity during observation of actions
Influence of action content and subject's strategy

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Summary
PET was used to map brain regions that are associated with the observation of meaningful and meaningless hand actions. Subjects were scanned under four conditions which consisted of visually presented actions. In each of the four experimental conditions, they were instructed to watch the actions with one of two aims: to be able to recognize or to imitate them later. We found that differences in the meaning of the action, irrespective of the strategy used during observation, lead to different patterns of brain activity and clear left/right asymmetries. Meaningful actions strongly engaged the left hemisphere in frontal and temporal regions while meaningless actions involved mainly the right occipitoparietal pathway. Observing with the intent to recognize activated memory-encoding structures. In contrast, observation with the intent to imitate was associated with activation in the regions involved in the planning and in the generation of actions. Thus, the pattern of brain activation during observation of actions is dependent both on the nature of the required executive processing and the type of the extrinsic properties of the action presented.

Keywords: action; observation; recognition; imitation; cognition; PET

Abbreviations: BA = Brodmann area; IF = observation of meaningful actions in order to imitate; IL = observation of meaningless actions in order to imitate; rCBF = regional cerebral blood flow; RF = observation of meaningful actions in order to recognize; RL = observation of meaningless actions in order to recognize; SPM = statistical parametric map

Introduction
Because understanding the meaning of a gesture is an essential aspect of human social communication, a large amount of our daily life is spent watching and interpreting the actions of others (Barresi and Moore, 1996). Each individual builds up from such observations his/her own theory of the thoughts/intentions of others. In addition, observation of actions is the first step of imitation, a powerful means of establishing contact with other individuals and acquiring new skills from them, which starts at birth and continues throughout life (Meltzoff and Moore, 1977).

It has been postulated that an observed action can be understood and imitated whenever it becomes the source of a representation of the same action within the observer. As a matter of fact, many arguments indicate that recognition of actions of the same species is a genuine ability, which seems to be highly developed in humans and non-human primates (Premack and Woodruff, 1978). Humans can easily distinguish biological motion from that produced externally by mechanical devices, even when only a limited number of cues are available (Johansson, 1973). Viviani and Stucchi (1992) expanded these findings by showing that perceptual estimation of curvilinear trajectories follows the same rules as the production of these trajectories by the motor system. They concluded that perception of actions is constrained by the implicit knowledge that the central nervous system has concerning the movements that it is capable of producing itself. This interpretation is remindful of the influential 'motor theory of perception' initially used to account for the perception of speech (e.g. *see* Liberman and Mattingly, 1985).

Results obtained in monkey experiments reinforce this idea. Perrett and his coworkers (1990) have disclosed, within the superior temporal sulcus, neuronal populations which appear to be involved, not only in the recognition of body postures (some neurons are more active when the animal is shown the hand or the head of another monkey in a given posture; Perrett *et al*., 1989), but also in the recognition of actions. Neurons are selective for movements in a particular direction when they are produced by another monkey, whereas

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they remain silent if these movements are the consequence of the animal's own action (Perrett *et al*., 1990). Goal-directed actions are also coded by neurons selective for the observation of specific hand–object interactions, such as reaching, manipulating or holding (Perrett *et al*., 1989). Another group of neurons located in the region of the premotor cortex also have interesting properties in this respect. In striking contrast with the temporal neurons, however, they are selective both for the monkey's active performance of a particular type of hand movement and for the monkey's observation of the same hand movement made by an experimenter or by another animal ('mirror neurons'; di Pellegrino *et al*., 1992; Gallese *et al*., 1996). There are indications that a similar mechanism for matching observation and execution of actions might also exist in man. Fadiga *et al*. (1995) asked subjects to observe grasping movements performed by an experimenter for 3 s. At the end of the observation period, a transcranial magnetic stimulus was applied to their motor cortex and responses were recorded from hand muscles. These responses were found to be selectively increased in those muscles which would have been activated if the subjects had actually performed the same movement. This result clearly demonstrates that observation of an action increases the excitability of neural structures involved in execution of that action.

Even though the different modalities of the same action, whether it is observed, mentally simulated or prepared for execution, activate common neural mechanisms, this does not imply that they rely on the same representations (Jeannerod and Decety, 1995; Crammond, 1997). Indeed, previous experiments using brain mapping techniques in normal subjects have demonstrated that mentally simulating and actually performing it (the action of grasping and picking an object) activate cortical areas which only partly overlap; in both conditions, the inferior parietal lobule (Decety *et al*., 1994; Stephan *et al*., 1995; Rizzolatti *et al*., 1996; Faillenot *et al*., 1997), the dorsal premotor cortex (Decety *et al*., 1994; Stephan *et al*., 1995; Grafton *et al*., 1996) and the primary motor cortex itself (Leornado *et al*., 1995; Roth *et al*., 1996) are involved. However, mental simulation also involves activation of ventral premotor cortex (Decety *et al*., 1994; Stephan *et al*., 1995; Grafton *et al*., 1996) which is not included in the execution network. Similarly, observing a grasping action and mentally simulating it activate different cortical areas. The inferotemporal cortex is activated during observation only (Decety *et al*., 1994), and the activated zones in the parietal, dorsolateral and ventral premotor cortices are clearly distinct in these two conditions (Grafton *et al*., 1996). These results stress the fact that different neural networks are activated when the representation of grasping movements is used with different cognitive strategies, such as observing, imagining or preparing the action towards an object.

However, an issue that has not been considered in these studies is the precise nature of the instruction given to the subject during the observation. Actions can be observed without being understood, because their meaning is not accessible to the observer. Yet, actions that are not understood can still be imitated. This raises the question of the relationship between perceptual recognition of an action as a spatiotemporal pattern and motoric recognition which will enable the observer to repeat this same action later on. The above motor theory of perception predicts that these functions should rely on a common representation which could subsequently be 'read' for different purposes, such as recognition or imitation. However, this cannot be true in situations where the observed action has an obvious meaning and is readily understood by the observer (like the pantomime of opening a bottle, for example). In this case, the action will probably be encoded, not only as a spatiotemporal pattern but also semantically, with the consequence that there will be two distinct representations for the same action. We all know that an action that is easily understood may not be easy to imitate; e.g. think of a backhand stroke played by a professional tennis player!

These remarks suggest that observed actions should have different neural correlates, regardless of whether they are unknown or familiar to the observer; and in addition, that the involvement of different brain areas should depend on the subject's strategy during observation. A model similar to that used for the neural representation of objects might also be used for actions. Different parts of the visual system have been shown to be involved depending on whether an object is represented 'for action' or 'for perception' (Goodale and Milner, 1992; 1993, Faillenot *et al*., 1997). Accordingly, distinct networks could be activated during observation of a meaningful action depending on whether (i) it is to be imitated and reproduced or (ii) it is to be categorized and identified. This distinction might be less clear for meaningless actions: in this case, the motoric encoding should predominate in both conditions, as one should expect that such actions cannot acquire a semantic status even if they have been learned and practised.

The experiment described here was designed to evaluate the pattern of neural activity during observation of actions where both the cognitive strategy of the subjects during observation and the semantic content of the actions were manipulated. The cognitive strategy was manipulated by instructing the subjects to prepare for later imitation, or later recognition of the observed action. The semantic content was manipulated by presenting two types of actions. Actions of the first type were meaningful actions which referred to a recognizable goal; those of the second type were meaningless sequences of actions with a similar content in terms of kinematics and degree of motor complexity.

Material and methods

Subjects

Ten males (22–24 years old) who had given their informed consent participated in the experiment. All were right-handed

Table 1 *Four scanning conditions repeated in each subject*

Nature of the stimulus	Task instruction	Abbreviation
Meaningful actions	Observation to imitate	IF
Meaningful actions	Observation to recognize	RF
Meaningless actions	Observation to imitate	IL
Meaningless actions	Observation to recognize	RL

according to the Edinburgh Inventory test (Oldfield, 1971). 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 Bérand). Subjects were paid for their participation.

Activation tasks

Subjects were scanned during the observation of video-filmed scenes. Four conditions were used according to the instructions given to the subjects (for definitions of the four conditions and their abbreviations—IF, IL, RF and RL—*see* Table 1). Each condition was repeated and performed in a counterbalanced order.

Prior to scanning, and after general instructions had been given, a few practice trials were administrated for each condition. The videos used in the practice trials were different from those used during the scanning period.

In all conditions, the video showed an experimenter enacting a sequence of five actions executed with the upper limb (showing the upper limbs and the trunk only). Each action lasted for 5 s and was separated from the next by a blank screen for 500 ms (*see* Fig. 1); each action was repeated three times within a random sequence (a total of 15 stimuli). The stimuli were presented in the centre of a colour video monitor (36 cm), located in front of the subject at 60 cm from their eyes. The screen was oriented 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.

The experimental conditions are represented diagrammatically in Fig. 1. In two conditions (RF and IF), meaningful actions were presented. The actions consisted of pantomimes (e.g. opening a bottle, drawing a line, sewing a button, hammering a nail) performed by a right-handed person. They mainly involved the right (dominant hand); the left hand was used to hold the imaginary object.

In two other conditions (RL and IL), meaningless actions were presented. These actions were derived from the American Sign Language with the constraints that they should be physically and perceptually as close as possible to the actions presented during the meaningful actions (e.g. movements involving mainly the right hand). As the subjects were unacquainted with the American Sign Language, they were unable to relate such actions to language or symbolic gestures.

For both types of actions (meaningful and meaningless), subjects were instructed to observe the videos carefully with one of two purposes: either to 'imitate' or to 'recognize' the actions.

When the purpose of the task was to 'observe in order to recognize' (conditions RF and RL), subjects were instructed that, at the end of the scanning acquisition, they would have to recognize the five actions that they had seen during the scan. The subjects' performance was assessed immediately after the scan by using a forced choice verbal response test, in which they had to recognize the five target actions out of 15 actions from another video film. In order to increase the task difficulty, as well as the attentional level, these actions were only slightly different from those presented during the PET acquisition period.

When the purpose of the task was to 'observe in order to imitate' (conditions IF and IL), subjects were instructed that they would have to reproduce the five actions that they had seen during the scan accurately. The subjects' performance was recorded on a videotape and then scored on a three-point scale (2 = correctly reproduced action; 1 = incorrectly reproduced action; 0 = not reproduced). The scores were then converted into percentages (of correct responses).

In all experimental conditions, as well as during both tests after scanning, the subjects were specifically instructed to avoid verbalization.

Finally, in order to assess the degree of effort that subjects experienced during the execution of the experiment, they were asked, at the end of the whole scanning session, to rate their subjective sensation of effort on a seven-point rating scale (1 = easy; 7 = difficult). A *post hoc* questionnaire was administrated to the subjects after the scanning procedure in order to know which strategy they used during the observation phase.

The general ability of the subjects to recognize, or to imitate, the selected stimuli had been evaluated prior to the scanning experiment on another group of 10 subjects. For these subjects, the same videos (meaningful and meaningless actions) were displayed and their performance in imitation and recognition tasks was recorded in the same way as for the PET study.

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 the 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 look at the monitor comfortably.

The PET tomograph was a GE-Advance (General Electric Medical System, Milwaukee, Wisc., USA) with collimating septa retracted to achieve optimal sensitivity (DeGrado *et al.*,

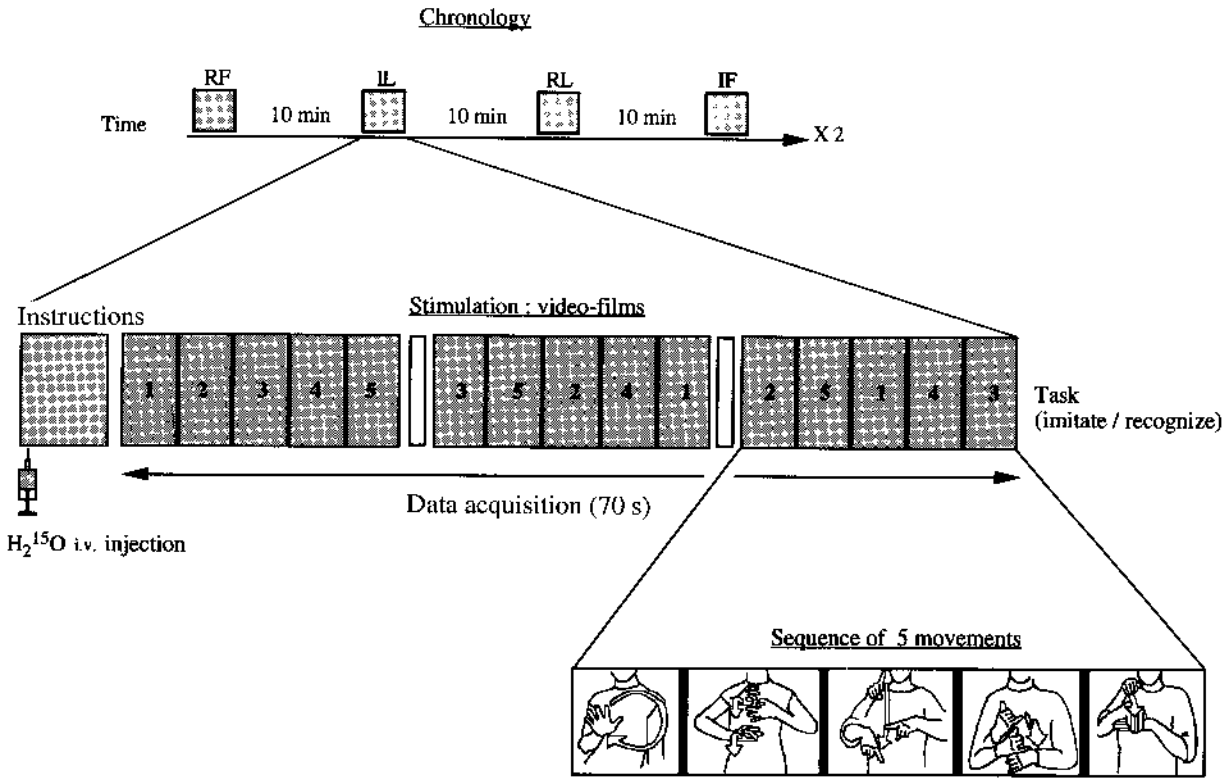


Fig. 1 Task design used for all experimental conditions. Note that the scanning acquisition (70 s) was only made during the observation phase. Imitation or recognition tasks were performed by the subjects immediatly after the completion of data scanning acquisition. Examples of five meaningless actions are given as an illustration at the bottom of the figure.

1994). The system has 18 rings which allows the acquisition of 35 transaxial images with a slice thickness of 4.25 mm covering an axial field of view of 15.2 cm. Transmission data were acquired using a pair of rotating pin sources filled with ^{68}Ge (10 mCi/pin). A filtered back-projection algorithm was employed for image reconstruction, on a 128×128 matrix with a pixel size of 1.9 mm, using a Hanning filter in the transaxial plane (cut-off width 4 mm) and a ramp filter (cut-off 8.5 mm) in the axial direction. In the stereotaxic standard space, each voxel was 2×2×4 mm in size. Regional cerebral blood flow (rCBF) was estimated by recording the distribution of radioactivity following an intravenous bolus injection of 1110 MBq of ^{15}O-H2O through a forearm cannula placed into the brachial vein. The integrated counts collected for 70 s, starting 20 s after the injection, were used as an index of rCBF.

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

PET image analysis

Image analysis was performed in MATLAB 4.2 (Math Works, Natick, Mass., USA) using the software for statistical parametric mapping (SPM95, MRC Cyclotron Unit, London, UK; Friston *et al.*, 1995). Individual PET data were oriented along the intercommisural line using an averaged image from each subject, and then transformed into a standard stereotaxic space (Talairach and Tournoux, 1988). 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 activation significant at $P < 0.0005$, uncorrected for multiple comparisons ($Z > 3.30$), were considered. Activated foci above a *Z*-threshold of 4.25 correspond to a corrected $P < 0.05$ for multiple comparisons. The activation foci were superimposed on anatomical structures from a stereotactically normalized averaged MRI atlas.

The figures show the different statistical analyses of the distribution of rCBF which were performed.

Main effects

Main effects were estimated relative to: (i) strategies used during the observation of actions (to recognize or to imitate), according to the formulae [(RF + RL) – (IF + IL)] and [(IF + IL) – (RF + RL)], respectively; and (ii) the nature of the stimuli (meaningful or meaningless actions), according to the formulae [(RF + IF) – (RL + IL)] and [(RL + IL) – (RF + IF)], respectively.

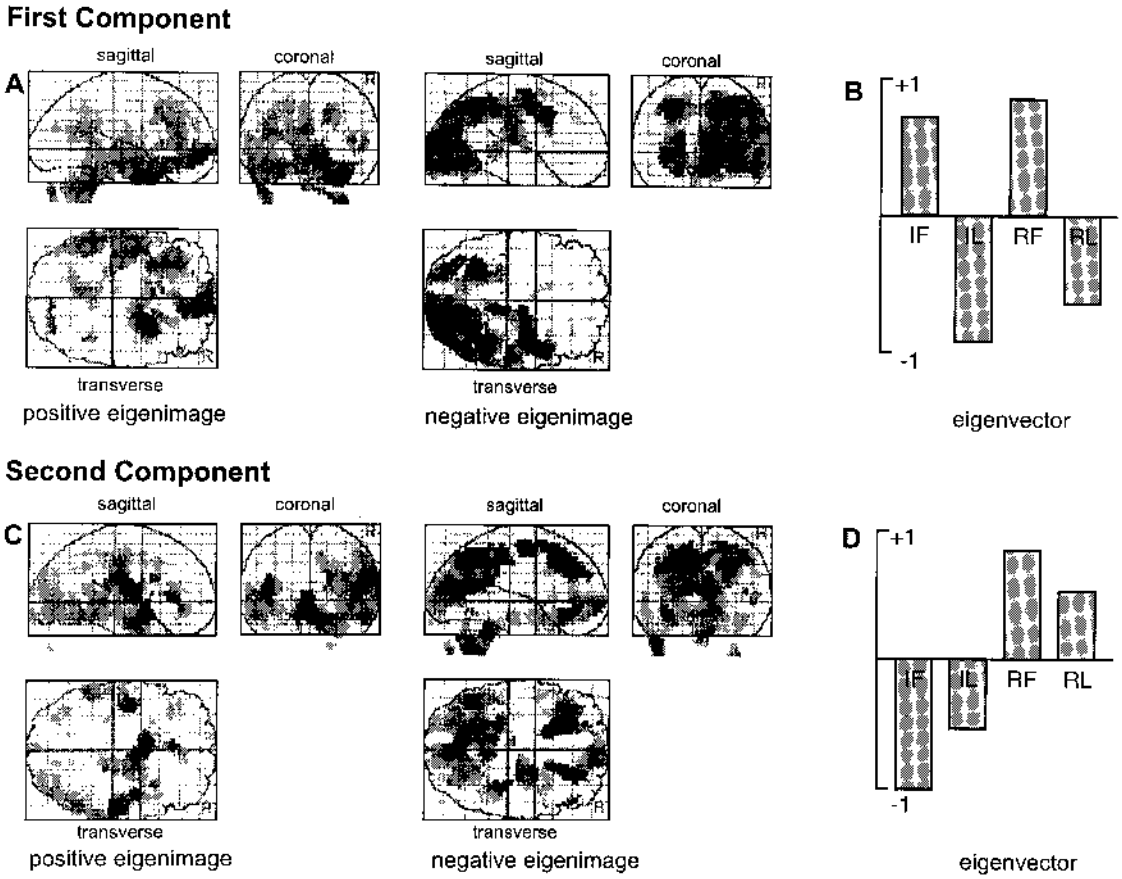


Fig. 2 The first two components of the principal component analysis performed on the four activation conditions (IF, IL, RF and RL). The first component accounts for 51% of the variance. (**A**) Pattern of positive (IF and RF, meaningful actions) and negative (IL and RL, meaningless actions) covariance of the first component (eigenimages). (**B**) Condition-dependent profile of the first component (eigenvector). The second component accounts for 22.5% of the variance. (**C**) Pattern of positive (recognition task) and negative (imitation task) covariance of the second component (eigenimages). (**D**) Condition-dependent profile of the second component.

Simple main effects

Simple main effects were: (i) observation of meaningful actions versus meaningless actions in order to recognize (RF – RL); (ii) observation of meaningful actions versus meaningless actions in order to imitate (IF – IL); (iii) observation of meaningless actions versus meaningful actions in order to recognize (RL – RF); and (iv) observation of meaningless actions versus meaningful actions in order to imitate (IL – IF).

Principal component analysis

A singular value decomposition was used to divide the original data set into a series of independent components with decreasing contributions to the variance in the voxel values. For each component, the singular value decomposition supplies three parameters: (i) an eigenimage, i.e. a pattern of covariation structures that can be displayed as a brain image; (ii) an eigenvalue which is the 2-norm of the eigenimage and gives also the proportional contribution of that component to the global variance, and (iii) a condition-dependent profile called eigenvector which represents its influence on the different conditions of activation. This decomposition leads to the principal component analysis. Knowing that the components are independent of each other, they can be viewed as independent factors of variance. The profile of the eigenvector of the components is the most relevant indication for attributing the function which causes the variation. Eigenimages are divided into positive and negative images for a more readable presentation; conditions whose contribution is positive are represented by a corresponding positive eigenimage and those whose contribution is negative are represented by negative images (for a complete description of this analysis, *see* Friston *et al*., 1993).

Results

Subjects' performance

The subjects achieved 95% correct in the recognition tasks (RF, 92%; RL, 97%) and 72% in the imitation tasks (IF, 77%; IL, 67.5%). Concerning their subjective sensation of effort, recognition tasks were evaluated as easier (RF, 1.5/7 and RL, 2.7/7), whereas subjects scored the imitation tasks as rather difficult (IF, 5/7 and IL, 6/7). Overall, subjects'

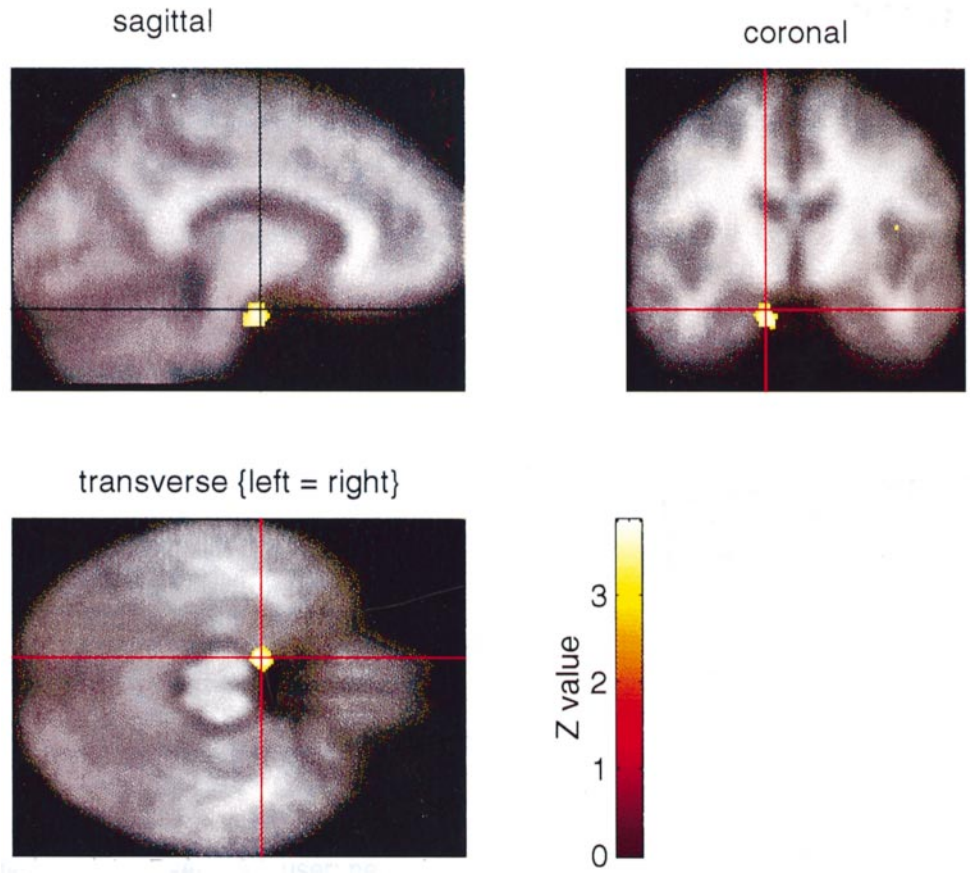


Fig. 3 rCBF increase in the region corresponding to right parahippocampal gyrus (BA 28) during observation of meaningful actions versus meaningless actions in order to recognize, overlaid on an averaged MRI scan.

performance was similar to that of the subjects who were studied prior the scanning experiment.

Responses from the questionnaire indicated that during observation of meaningful actions, the subjects associated rather automatically a semantic content but that they also paid careful attention to the actions displayed in term of visuospatial encoding. In contrast, during observation of meaningless actions, they did not associate a semantic content, and mainly used a visuospatial analysis.

PET results

The results from the principal component analysis will be presented first. Then, the main effects relative to the strategies used during observation of actions (to imitate or to recognize), irrespective of the nature of the stimulus, and those relative to the nature of the stimuli (meaningful or meaningless actions), irrespective of the strategy used, will be presented. Finally, simple main effects relative to comparisons between conditions will be described.

Principal component analysis

A Principal Component Analysis was performed on the whole data set (Fig. 2). This analysis confirms that the first two components, accounting for 73.5% of the variance, were linked with the cognitive factors that were introduced by the stimuli (meaningful/meaningless) and by the instructions (imitate/recognize) given to the subjects. The first component, which represents 51% of the variance, characterizes the different neural structures involved in the observation of meaningful and meaningless actions. The positive eigenimage (meaningful conditions) mainly engaged the left frontal and temporal lobes. In contrast, the negative eigenimage (meaningless conditions) engaged the right occipitoparietal regions. The second component represents 22.5% of the variance. The corresponding eigenimage shows the localization of the activations that are due to the tasks required during observation (imitate or recognize).

Main effect related to the cognitive strategy during observation of actions

The results of these SPM analyses are presented in Table 2. Observing in order to recognize actions, irrespective of their content (meaningful or meaningless) produced a strong activation of the right parahippocampal gyrus (*see* Fig. 3).

Observing in order to imitate actions, irrespective of their

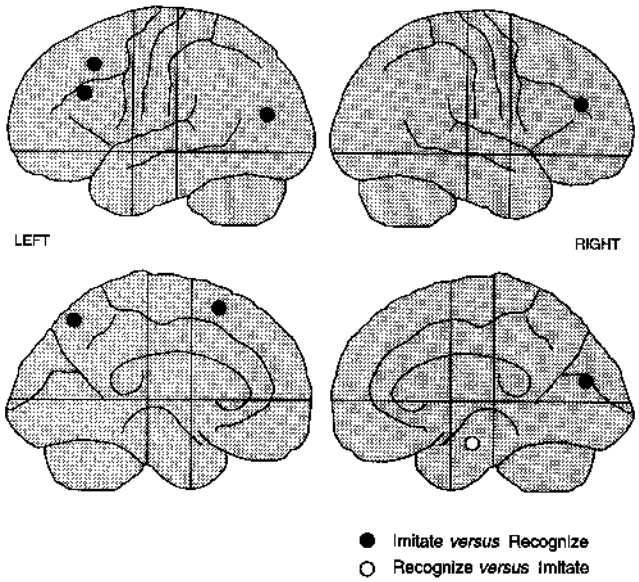


Fig. 4 Cerebral localization of activated areas during the observation of actions, depending on the subject's strategy (in order to recognize and imitate), irrespective of the nature of the stimuli. Lateral views are shown on the top, and medial views on the bottom of the figure. Results correspond to Table 2.

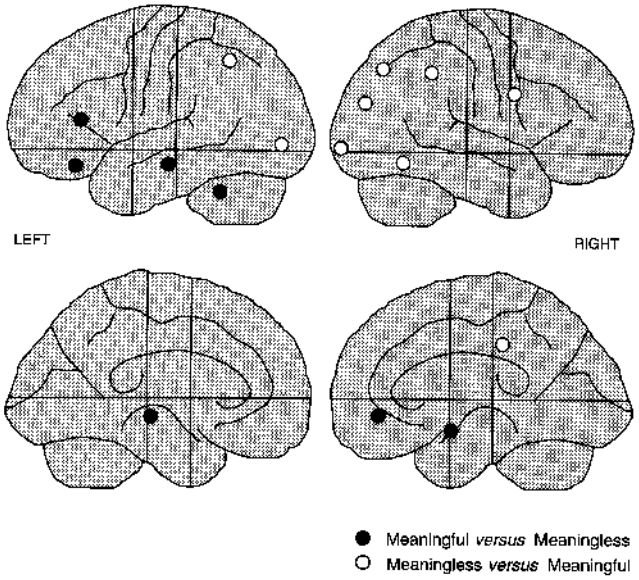


Fig. 5 Cerebral localization of activated areas during the observation of meaningful and meaningless actions, irrespective of the strategy. Results correspond to Table 4.

content was associated with rCBF increases in the dorsolateral prefrontal cortex bilaterally [Brodmann area (BA) 9] and in the left anterior supplementary motor area (pre-supplementary motor area). The middle occipital gyrus and the precuneus (BA 19 and 7) were also activated in the left hemisphere, whereas the cuneus (BA 18) was activated on the right side (*see* Fig. 4).

Main effect related to the content of observed actions

The results of these SPM analyses are presented in Fig. 5 and in Table 3. The rCBF increases during observation of meaningful actions, as opposed to meaningless actions, irrespective of the strategies used by the subjects, were located mainly in the left hemisphere. Activated regions included the left inferior frontal gyrus (BA 45 and 47) and the left middle temporal gyrus (BA 21). The cerebellum was also activated on the left. The hippocampal gyrus was bilaterally activated. The orbito frontal gyrus (BA 11) was activated in the right hemisphere.

Activation produced by the observation of meaningless actions, as opposed to meaningful actions, irrespective of the subjects' strategies were mainly located in the right hemisphere. The right occipitoparietal pathway (BA 18, 19, 7 and 40) and the right ventral premotor cortex (BA 6) were activated. In the left hemisphere activations were also found in the cuneus (BA 18) and in the superior parietal lobule (BA 7) (Fig. 5 and Table 3).

Simple main effect related to the observation of meaningful actions in order to recognize

The direct comparison of the observation of meaningful actions versus meaningless actions in order to recognize (RF – RL) showed a selective activation left hemispheric regions, in particular, the inferior frontal (BA 45), the inferior temporal (BA 20/37) and the middle temporal (BA 21) gyri (Table 4). The parahippocampal, the posterior cingulate and the middle frontal gyri, as well as the cerebellum, were also activated on the left side.

Simple main effect related to the observation of meaningful actions in order to imitate

The simple main effect due to the observation of meaningful versus meaningless actions in order to imitate (IF – IL) was associated with activation in the left inferior frontal (BA 47) and the left middle temporal (BA 21) gyri. The medial frontal (BA 11) and the parahippocampal (BA 28/34) gyri were activated in the right hemisphere. An activation focus was found in the left cerebellar hemisphere (Table 4).

Simple main effect related to the observation of meaningless actions in order to recognize

The observation of meaningless versus meaningful actions in order to recognize (RL – RF) was associated with activations in the cuneus (BA 18) bilaterally and in the inferior parietal lobule (BA 40) on the right. In addition, the right occipitotemporal junction (BA 19/37) appeared to be involved (Table 5).

Table 2 *Brain regions with significantly increased rCBF associated with the task (intention to imitate or recognize) during observation of actions, irrespective of their meaning*

Brain region	Hemisphere	BA	Coordinates			*Z*-score
			x	*y*	*z*	
Imitate versus recognize						
Medial frontal gyrus (pre-SMA)	L	6	–10	14	52	3.71
Precuneus	L	7	–10	–66	44	3.77
Middle frontal gyrus	L	8	–22	22	44	4.08
Middle frontal gyrus	L	9	–38	28	32	4.41
Middle frontal gyrus	R	9	24	38	28	3.56
Middle occipital gyrus	L	19	–34	–74	20	4.02
Cuneus	R	18	4	–78	16	3.77
Recognize versus imitate						
Parahippocampal gyrus	R	28	12	–10	–20	3.69

Coordinates are in millimetres, relative to the anterior commissure, corresponding to the Talairach and Tournoux atlas. L = left; R = right; SMA = supplementary motor area. Threshold at $Z = 3.30$ ($P < 0.0005$).

Table 3 *Brain regions with significantly increased rCBF during observation of actions irrespective of the strategy/task*

Brain region	Hemisphere	BA	Coordinates			*Z*-score
			x	*y*	*z*	
Meaningful versus meaningless actions						
Inferior frontal gyrus	L	45	–36	32	16	4.15
Medial frontal cortex	R	11	12	42	–12	4.42
Middle temporal gyrus	L	21	–50	–20	–8	5.10
Inferior frontal gyrus	L	47	–28	30	–12	4.03
Hippocampal gyrus	L	28	–40	–22	–12	4.22
Hippocampal gyrus	R	28	24	0	–24	4.64
Cerebellum	L		–54	–48	–24	4.43
Meaningless versus meaningful actions						
Inferior parietal lobule	R	40	46	–48	44	4.89
Superior parietal lobule	L	7	–28	–56	44	3.78
Superior parietal lobule	R	7	22	–72	44	4.79
Precentral gyrus	R	6	44	4	36	3.98
Superior occipital gyrus	R	19	26	–84	28	4.92
Cuneus	R	18	12	–100	4	5.38
Cuneus	L	18	–28	–84	4	3.47
Inferior temporal gyrus	R	37	50	–64	–4	3.79

See footnote to Table 2 for details.

Simple main effect related to the observation of meaningless actions in order to imitate

Comparable areas in the right hemisphere, within the occipitoparietal regions (inferior parietal lobule and occipitotemporal junction) were activated during observation of meaningless versus meaningful actions in order to imitate (IL – IF) (Table 5). The right precuneus (BA 7) and the ventral premotor region (BA 6) were also activated.

Discussion

Influence of the cognitive strategy used during observation

One of the most striking finding of this study was that the pattern of brain activation during tasks based on the same visual stimuli (familiar or nonfamiliar actions) changed according to the cognitive task in which the subject was involved. When the subject had to memorize familiar actions with the purpose of preparing to identify them among others, the right parahippocampal gyrus was the only activated area. In contrast, when the aim of observation was to memorize actions with the purpose of imitation, the activation was predominantly in structures that are usually involved in action planning.

The role of the parahippocampal region during the 'recognition' strategy was revealed by the statistical analysis used for comparing strategies irrespective of content (*see* Table 2). The activation predominated on the right side, although it was bilateral when the observed action was familiar. Our present knowledge of the role of this region is based on neuropsychological studies in patients with lesions

Table 4 *Brain regions with significantly increased rCBF during observation of meaningful actions with strategies enabling recognition and imitation*

Brain region	Hemisphere	BA	Coordinates			*Z*-score
			x	*y*	*z*	
Meaningful versus meaningless actions observed in order to recognize						
Posterior cingulate gyrus	L	30	–2	–48	20	3.44
Middle frontal gyrus	L	46	–38	28	24	3.57
Inferior frontal gyrus	L	45	–36	32	16	3.97
Middle temporal gyrus	L	21	–54	–26	0	3.86
Parahippocampal gyrus	L	28/35	–26	–32	–8	3.42
Inferior temporal gyrus	L	20/37	–56	–40	–20	3.70
Cerebellum	L		–48	–52	–36	3.67
Meaningful versus meaningless actions observed in order to imitate						
Middle temporal gyrus	L	21	–50	–10	–8	4.73
Medial frontal gyrus	R	11	12	42	–12	3.68
Inferior frontal gyrus	L	47	–30	24	–12	3.87
Parahippocampal gyrus	R	28/34	26	0	–20	3.93
Cerebellum	L		–46	–38	–28	3.48

See footnote to Table 2 for details.

Table 5 *Brain regions with significantly increased rCBF during observation of meaningless actions with strategies enabling recognition and imitation*

Brain region	Hemisphere	BA	Coordinates			*Z*-score
			x	*y*	*z*	
Meaningless versus meaningful tasks observed in order to recognize						
Inferior parietal lobule	R	40	46	–44	44	3.59
Cuneus	L	18	–26	–92	4	3.73
Cuneus	R	18	12	–100	4	4.64
Occipital temporal junction	R	19/37	48	–74	–8	4.07
Meaningless versus meaningful tasks observed in order to imitate						
Inferior parietal lobule	R	40	54	–48	36	4.02
Precuneus	R	7	18	–74	40	4.52
Precentral gyrus	R	6	48	6	36	3.61
Occipital temporal junction	R	18/37	36	–88	–8	3.88

See footnote to Table 2 for details.

of medial temporal lobe structures. These studies indicate that the hippocampal region is important for rapidly acquiring and storing new information about facts and events, which are then available to conscious recollection (Squire and Knowlton, 1995; Ungerleider, 1995). However, previous PET studies have rarely been successful in activating medial temporal areas in declarative memory tasks (especially those involving language, e.g. *see* Shallice *et al*., 1994). In contrast, our finding of a large and isolated parahippocampal activation when new action-related information had to be acquired for later recognition is in good agreement with the neuropsychological findings.

During the 'imitation' strategy, the dorsolateral prefrontal cortex on both sides and the pre-supplementary motor area were activated. The bilateral involvement of dorsolateral prefrontal cortex in this condition is an interesting finding. First, it is in agreement with previous studies concerning the planning of voluntary actions (Frith *et al*., 1991) and the mental simulation of actions (Decety *et al*., 1994; Stephan *et al*., 1995; Grafton *et al*., 1996). Secondly, involvement of dorsolateral prefrontal cortex, especially on the left side, was frequently observed during tasks, such as word generation (Frith *et al*., 1991; Wise *et al*., 1991) or verbal encoding (Shallice *et al*., 1994), which require access to semantic representations. Finally, Shallice *et al*. (1994) reported activation of the right dorsolateral prefrontal cortex in memory processes, during a semantic retrieval task. Thus, it could well be the case that the left prefrontal region would be specialized for generating responses in relation to semantic cues, whereas the right side would be more important for memory and the two sides would equally contribute to the more general function of internal response generation in all sorts of situations. The latter suggestion would fit our results, where the activation of the dorsolateral prefrontal cortex in both sides was only found during observation in order to imitate, irrespective of the nature of the actions presented, and not with the meaningful versus meaningless subtraction.

The involvement the left pre-supplementary motor area during the imitation strategy was an expected finding. It seems logical to assume that this part of premotor cortex,

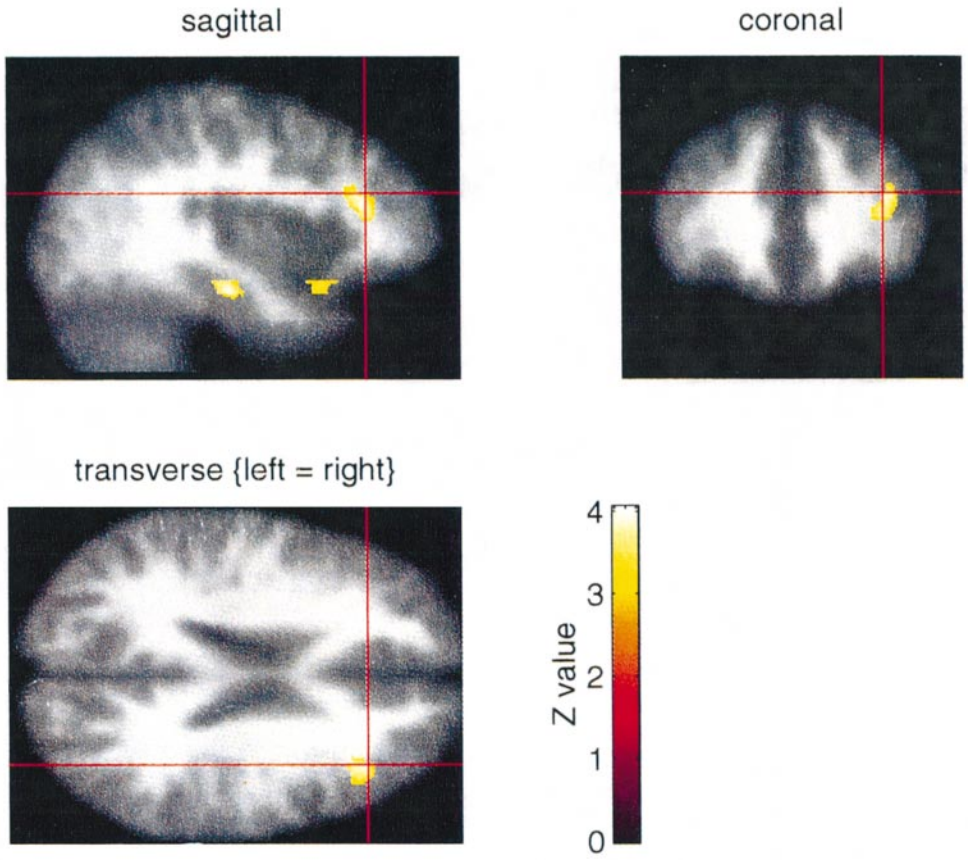


Fig. 6 rCBF increase in the region corresponding to left inferior frontal gyrus (BA 45) during observation of meaningful actions versus observation of meaningless actions irrespective of the strategy, overlaid on an averaged MRI scan.

which has a recognized function in motor memory and sequencing (Passingham, 1993, 1996; Tanji and Shima, 1994), should be involved when the subject was preparing to act. The fact that it was also reported to be active during observation of actions (Grafton *et al*., 1996) and during certain types of mental simulation of actions (Parsons *et al*., 1995; Stephan *et al*., 1995; Grafton *et al*., 1996; Roth *et al*., 1996), a condition which has many features in common with action preparation and planning, is consistent with our finding.

Influence of the content of observed actions: meaningful actions

The second major finding of this study was that the pattern of activation differed according to whether the observed action was meaningful or meaningless. Observing a meaningful action caused a prevalent activation of the left hemisphere (Fig. 2). This was true when meaningful actions were compared with meaningless ones, irrespective of the strategy used by the subjects during observation. The structures involved in the left hemisphere were the inferior frontal gyrus (BA 45), middle temporal gyrus (BA 21), parahippocampal regions and orbitofrontal regions (BA11 and 47) in both hemispheres.

Activation of area 45, as it is shown in Fig. 6, seems particularly relevant. This result must be compared with those of Grafton *et al*. (1996) and Rizzolatti *et al*. (1996) who also reported activation of the left inferior frontal gyrus, predominating in area 45 during observation of grasping movements. They conjectured that this region corresponds to a system for representation of grasping movements, functionally similar to ventral area 6 in the monkey, where 'mirror' neurons were recorded. Indeed, the same region is activated during mental simulation of hand actions (Decety *et al*., 1994; Grafton *et al*., 1996). An involvement of BA 45 in the left inferior frontal gyrus was also shown in a recognition task of man-made tools (Perani *et al*., 1995); the authors raised the principal hypothesis of associations linked to object manipulation and functional knowledge of the tools. Activation of the inferior frontal gyrus also raises the problem of the involvement of language during the observation of meaningful actions. Several authors have reported activation of this area in situations related to language concerned with action, such as generation of action words (Martin *et al*., 1995) or naming man-made tools (Martin *et al*., 1996). It is indeed a possibility that during the observation conditions, our subjects recognized the actions and automatically associated them with action verbs or with the name of the objects evoked by the actions. In fact, activation of area 45 (in conjunction with area 44) was observed in many 'verbal'

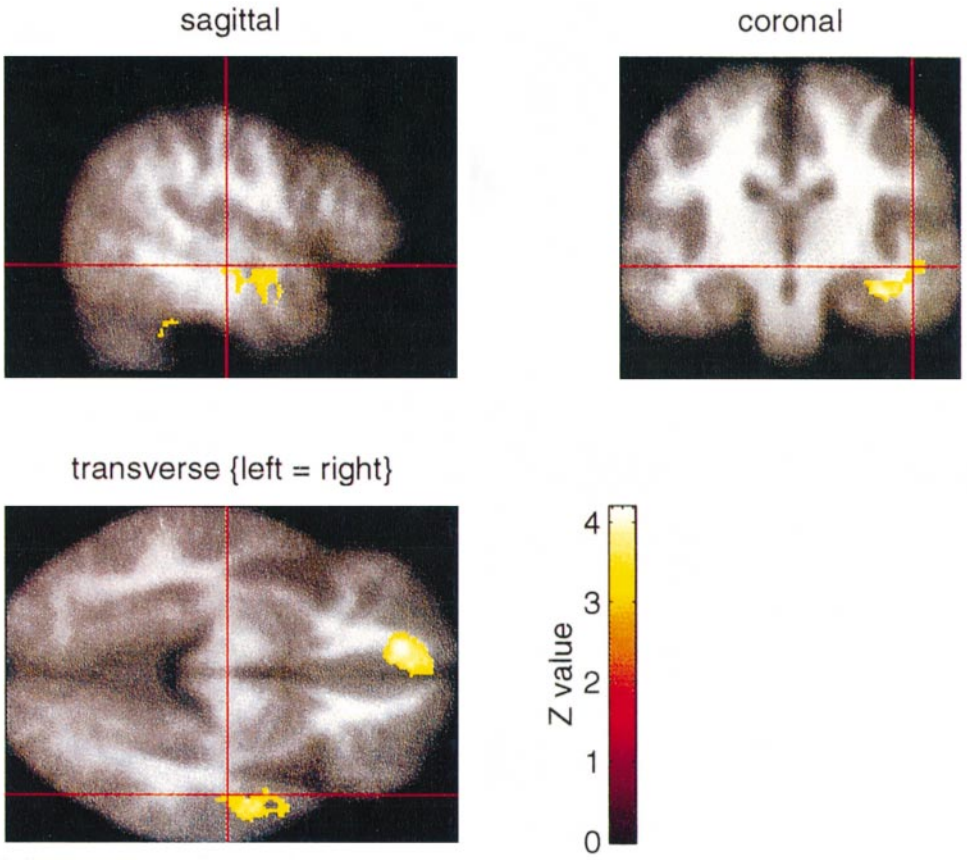


Fig. 7 rCBF increase in the region corresponding to left BA 21 during observation of meaningful actions versus observation of meaningless actions irrespective of the strategy, overlaid on an averaged MRI scan.

situations such as verb retrieval (Warbuton *et al*., 1996), silent word generation (Wise *et al*., 1991; McGuire *et al*., 1996) and lexicosemantic tasks (Demonet *et al*., 1992). In the present study, the inferior frontal activation was restricted to BA 45. It should be pointed out that BA 44 and 45 do not have the same cytoarchitectonic characteristics and their respective functions are not yet well established. The activation of this region in the left inferior frontal gyrus may be interpreted as reflecting an involvement in action recognition, as already suggested by Rizzolatti *et al*. (1996a) and Carey *et al*. (1997) rather than reflecting (solely) speech processing.

Another area, in the anterior part of the left middle temporal gyrus, corresponding to BA 21, was also involved during the observation of meaningful action (Fig. 7).

Activation of this area may be explained within the framework of recognition and memory storage of the semantic aspects of action, which is congruent also with our finding of an activation in the hippocampal and parahippocampal regions (Schacter *et al*., 1995). In fact, area 21 was also found to be activated in the above mentioned PET studies in which subjects generated action words or named tools (Martin *et al*., 1995, 1996; *see* also Wise *et al*., 1991). It is very tempting to establish an homology between the left area 21 in man and areas located in the superior temporal sulcus in the monkey. In this region, neurons are activated by object features (*see* Nakamura and Kubota, 1996) and are also selectively responsive to the sight of actions performed by the hand (Perret *et al*., 1989; Carey *et al*., 1997).

Activation of area 21 must be discussed in relation to the effects of temporal lesions in man. These lesions typically impair recognition of objects (object agnosia), a deficit which may sometimes predominate for certain object categories (e.g. 'man-made' versus 'natural' objects; Warrington and Shallice, 1984). Sirigu *et al*. (1991) reported such a case after bilateral lesion of temporal poles. However, their patient, when shown usual but unrecognized objects, was still able to make the proper gestures to use them. This remarkable dissociation indicates that correct representations for the use of objects can be formed and can operate independently of temporal cortex. Returning to our experiment, the suggestion can be made that observation of meaningful actions, although no actual objects were presented (only suggested by the pantomimes) resulted in activation of areas involved in semantic object processing (temporal area 21) and action recognition (inferior frontal area 45).

Another area, within the orbitofrontal region (BA 11 and 47), was activated during observation of meaningful action

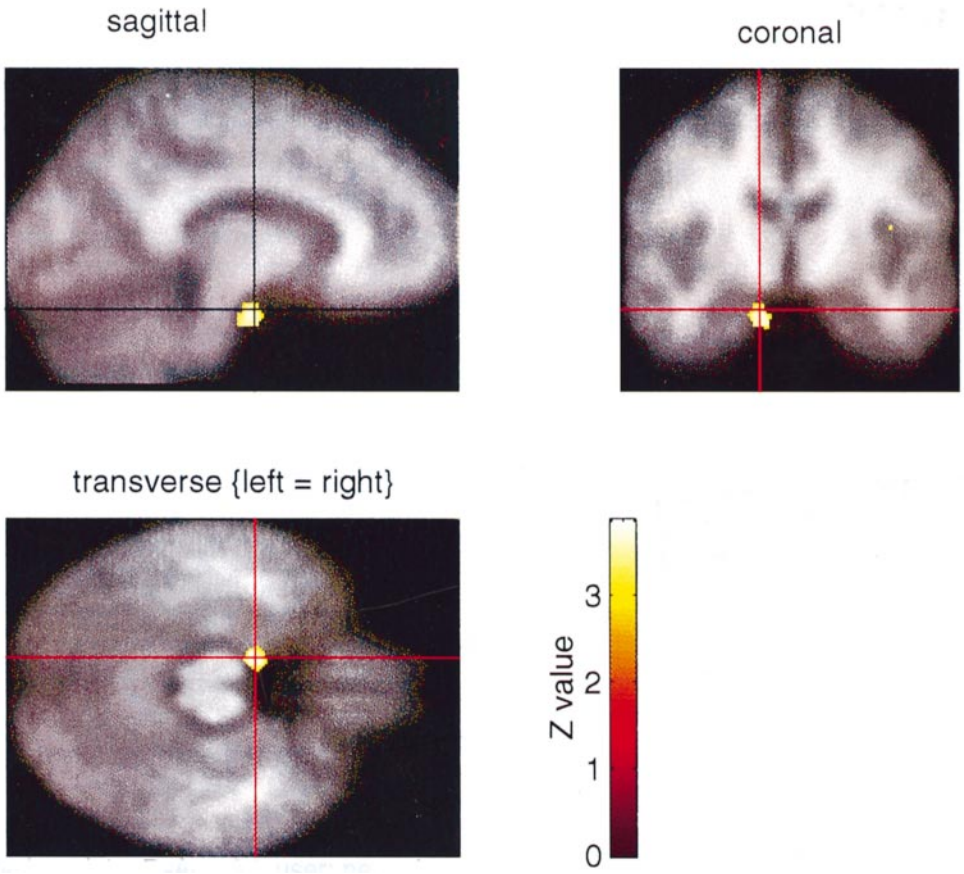


Fig. 8 rCBF increase in the region corresponding to right ventral BA 6 during observation of meaningless actions versus observation of meaningful actions, overlaid on an averaged MRI scan.

in order to imitate. The role of this activation could be interpreted as an inhibition of the actions which have to be reproduced later. Indeed, patients with lesions of this part of the frontal cortex may exhibit an exaggerated dependence on environmental cues (the so-called utilization behaviour), which has been interpreted as a consequence of impaired inhibition of automatic, externally triggered actions (Lhermitte *et al*., 1986).

Activation could have been expected in the parietal cortex since this region is known to play a key role in action representation (Rothi *et al*., 1991; Sirigu *et al*., 1995, 1996). In a recent PET study during perception of biological motion, Bonda *et al*. (1996) reported involvement of the parietal cortex during perception of hand action. The lack of detection of this cortical region in our study may be a consequence of the subtractions between conditions which all included hand movements.

Influence of the content of observed actions: meaningless actions

In contrast with the observation of meaningful actions, which mostly involved structures located in the left hemisphere, observation of meaningless actions primarily engaged the right hemisphere. This activation involved areas in the occipitoparietal region, including the cuneus and the precuneus, the middle occipital gyrus and the inferior parietal lobule. In addition, the inferior temporal gyrus was involved as well as the ventral premotor cortex.

The predominant activation of right occipitoparietal areas in this condition fits the role of this visual pathway for processing the spatial properties of visual scenes and for generating visuomotor transformation. Recent experiments using PET in normal subjects showed activation of the right occipitoparietal cortex during tasks involving spatial vision (Haxby *et al*., 1994, Kosslyn *et al*., 1994, Faillenot *et al*., 1997). Accordingly, right posterior parietal lesions in man are known to produce visuospatial deficits such as spatial disorientation, spatial neglect or constructional apraxia (Heilman *et al*., 1986; De Renzi, 1989; Lezak, 1995). In addition, lesions on either side can produce deficits in visuomotor transformation, such as misreaching and lack of finger preshaping during the action of grasping objects (Jeannerod, 1986, Perenin and Vighetto, 1988). The fact that this region was strongly activated supports the role of inferior parietal lobule in the processing of novel movements patterns, as it has already been reported (Jenkins *et al*., 1994).

When observation of meaningless actions was performed

in order to imitate, a region of the precentral gyrus corresponding to the right lateral premotor cortex (BA 6) was activated (*see* Fig. 8).

This fact is consistent with the activation of parietal areas, such as BA 40. The region of the intraparietal sulcus in the monkey is known to be connected with premotor cortex; direct connections between area 7b, which might correspond to the human area 40, and the ventral area 6, have been demonstrated in monkeys (Petrides and Pandya, 1984). Joint activation of areas 40 and 6 during preparation for imitation would thus account for transferring the processing of novel movement patterns into a motor code.

Conclusion

The results obtained in this study, during observation of actions, clearly demonstrate that the two types of action lead to activation of different neural networks. Indeed, the pattern of cortical activation corresponding to these two types differ both in terms of hemispheric asymmetry and repartition of the involved areas. The network activated during observation of meaningful actions in the left hemisphere corresponds to the 'ventral' visual pathway, which includes inferotemporal areas, part of the hippocampus and terminates in the ventral part of prefrontal cortex. On the other hand, the network associated with meaningless actions in the right hemisphere corresponds mainly to the 'dorsal' pathway, which includes occipitoparietal areas and is connected with premotor cortex and also regions within the ventral pathway, namely the cuneus and the inferior temporal gyrus. Thus, the ventral stream also contributes during the observation of meaningless actions.

The fact that unfamiliar actions can only be decoded in terms of their spatiotemporal layout, which includes direction of movements in three-dimentional space and kinematics, is consistent with a predominant activation of the dorsal pathway. In contrast, actions with a semantic content, especially if they refer to objects, must be processed by areas which enable access to meaning and memory storage.

Furthermore, the fact that the cognitive strategy used by the subjects involved specific brain regions suggests a selective processing of information during the perception of actions.

Finally, our results demonstrate that observation is a selective process that recruits neural networks depending both on the nature of the action perceived and on the subject's purpose. They also provide some neurophysiological evidence to the observational theory of learning (Carroll and Bandura, 1982). As proposed recently by Vogt (1996) based on psychophysical experiments, the perception–action link relies on motor representations which are already activated (or formed) during observation.

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