

The effects of learning and intention on the neural network involved in the perception of meaningless actions

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Summary

PET was used to explore the neural network involved in the perception of meaningless action. In two conditions, subjects observed learned and unknown meaningless actions without any purpose. In two other conditions, subjects observed the same type of stimuli for later imitation. The control condition, which consisted of the presentation of stationary hands, served as a baseline. Unsurprisingly, a common network that forms part of the dorsal pathway was engaged in all conditions when compared with stationary hands, and this was interpreted as being devoted to the analysis of hand movements. One of the most striking results of the present study was that some brain areas were strongly modulated by the learning level, independent of the subject's intention. Two different

effects were observed: a reduced activity in posterior regions within the common network, which correlated with specific increases in the frontopolar area 10 and in the angular gyrus during the perception of learned meaningless actions compared with the perception of unknown actions. Finally, the major effect of the subject's intention to imitate was a strong increase in the dorsal pathway extending to the lateral premotor cortex and to the dorsolateral prefrontal cortex, which reflects the information processing needed for prospective action. Overall, our results provide evidence for both an effect of the visuomotor learning level and of the subject's intention on the neural network involved during the perception of human meaningless actions.

Keywords: perception; intention; action; motor knowledge; PET

Abbreviations: BA = Brodmann area; rCBF = regional cerebral blood flow; SPM = statistical parametric map

Introduction

The idea that perception and action are intimately linked is not new. Indeed, Sperry proposed in 1952 that perception is basically an implicit preparation to respond, and even more, that its function is to prepare the organism for adaptive action (Sperry, 1952). Later, it was postulated by Konorski that when perceiving a movement, the brain formulates the commands that produce the corresponding voluntary movement (Konorski, 1967).

A recent revival of interest in the domain of perception of action has been motivated by the discovery in the monkey of neurons in the ventral premotor cortex (F5) that exhibit similar responses to the sight of a given action and to the execution of the same action (Gallese *et al.*, 1996). In humans, a similar mechanism may be postulated. In 1979, Berger and colleagues demonstrated by electromyography that observation of body movements is associated with specific innervation in the corresponding muscles (Berger

et al., 1979). Later, Fadiga and colleagues confirmed this result by applying transcranial magnetic stimulation to the motor cortex of subjects during observation of grasping movements (Fadiga *et al.*, 1995). Their results showed that there was a selective increase of motor evoked potential, recorded from hand muscles during the observation of actions.

More recently, functional imaging techniques have been applied with the aim of identifying the brain areas involved in the observation of actions. In two PET experiments, comparisons were made between subjects observing an experimenter grasping objects and object observation as a control (Grafton *et al.*, 1996; Rizzolatti *et al.*, 1996). The results demonstrated that grasp observation significantly activated the superior temporal sulcus, the inferior parietal lobule and the inferior frontal gyrus (BA 45). This latter region, along with the *pars opercularis*, constitutes the Broca's area, and is thought to be the homologue of monkey

F5 (Rizzolatti and Arbib, 1998). A similarly distributed network was found to be activated during the observation of meaningful pantomimes but not by meaningless movements (Decety *et al.*, 1997; Grèzes *et al.*, 1998). This suggests that the presence of the actual object is not requisite in activation in humans, but merely that its representation is sufficient to involve or evoke the whole action recognition network. Taken together, human and monkey data led Rizzolatti and Arbib to propose that individuals recognize actions made by others because the neural pattern elicited in their premotor areas (BA 45/F5) is similar to that internally generated to produce that action (Rizzolatti and Arbib, 1998). Jeannerod and Decety have also suggested a related model on the basis of mental simulation of action (Jeannerod, 1994; Decety, 1996). A very similar network, namely the activations in the left inferior frontal, superior temporal and inferior parietal gyri, are also found during various language activation tasks (e.g. Warburton *et al.*, 1996). It is thus conceivable that observation of actions stirs speech processes and, in particular, verb generation. Indeed, activations have been reported in the inferior frontal gyrus and in the temporal cortex during action word generation or on immediate recognition of visually presented objects and tools (Martin *et al.*, 1996; Grabowski *et al.*, 1998). Several clinical and experimental studies have shown that nouns and verbs can be independently disrupted by brain damage (Gainotti, 1998). Selective loss of verbs frequently has been observed in neurological patients. Broca's aphasics are mainly impaired in naming actions (producing verbs), whereas fluent aphasics show a prevalent impairment in naming objects (producing nouns).

Thus it is difficult to separate the putative involvement of language processes during the perception and the recognition of actions, or to assess to what extent covert speech processes affect the activated network. On the clinical side, it is acknowledged that apraxia is frequently associated with aphasia, although there is no clearly demonstrated causal link between the two symptoms (De Renzi, 1989). We suggest that another way to investigate the neural substrate underlying the putative direct link from perception to action, without language interference, is to use meaningless gestures. Such gestures are usually novel and are consequently not represented in the long-term motor memory.

It has been demonstrated that the learning level has an effect on the neural network during motor execution. Several PET studies have investigated the neuronal responses associated with different stages of learning (e.g. Roland *et al.*, 1991; Grafton *et al.*, 1992; Jenkins *et al.*, 1994; Jueptner *et al.*, 1997), and have suggested that the neural representation of motor function is dynamic. The acquisition of skilled movements seems to be mediated principally through structures in the prefrontal cortex, and then with time or practice, as the task becomes overlearned or automatic, motor structures assume a greater role and possibly become the site of motor memory. Shadmehr and colleagues demonstrated that within 6 h of completion of practice, new regions were engaged to perform the same motor task, namely that there

was a shift from prefrontal cortex to the premotor, posterior parietal and cerebellar cortex structures (Shadmehr *et al.*, 1997). Thus, with the passage of time, a reduction of activation within the prefrontal cortex coincident with activations in more posterior areas has been observed (Jenkins *et al.*, 1994; Jueptner *et al.*, 1997). Hence, there is a clear plasticity effect due to the learning level on the regions involved in motor output. To what extent would this effect be observed during the perception phase of actions? The answer to this question could provide additional evidence for theories that postulate a common coding between action and perception. It is possible to address specifically the issue of integration of visual information by contrasting the perceptions of learned and unknown meaningless movements. In order to dissociate the effect of familiarity (in the sense of learning or skilled) from the effect of the semantic content of actions, meaningless movements that have no semantic labelling must be used.

When a person perceives new movements, perception may refer to the movements of the body and the resulting trajectory of arms, whereas for well-practised meaningless movements that have no access, at least not explicitly, to semantic labelling, perception may refer to sensorimotor representations in long-term memory. These situations should be rather different from the perception of meaningful actions for which semantic knowledge may dominate over structure in the perception. However, it is not clear that learned meaningless actions do engage sensorimotor representations in the same sense as meaningful ones (i.e. goal and the means to achieve it). Within Prinz's theoretical framework (Prinz, 1997), meaningful actions would refer to the intended effect of the movement pattern (in reference to the intended effect) as well as to the meaning of the action, whereas learned meaningless actions would refer solely to the intended event pattern (reference to pattern).

Another interesting question deals with the subject's intention during perception. Indeed, it has been demonstrated previously that cortical regions involved in motor representation are already engaged during action perception (Decety, 1996). Are there any differences between actions that are novel and those that are already learned?

The present study was designed to investigate the effect of the familiarity through learning, using the perception of pre-learned versus unlearned meaningless movements on the neural network. The neural response to the perception of hand actions was assessed by measuring regional cerebral blood flow (rCBF) with PET in normal subjects while they observed meaningless actions without any purpose or actions with the intent to imitate them later.

Material and methods

Subjects

Nine healthy right-handed male volunteers (age range 23–36 years) participated. The handedness was assessed by the

Edinburgh Inventory test (Oldfield, 1971). Written informed consent was obtained in accordance with the guidelines from the Declaration of Helsinki and the approval of the local Ethical Committee (Centre Léon Bérard). Subjects were paid for their participation.

Learning phase

Before the PET experiment, subjects completed a 3-day learning period. The experimental task was to learn to accurately reproduce visually presented movements by delayed imitation. The movements to be learned consisted of 20 meaningless actions that were derived from American sign language with the aim to mainly involve the right hand. Because the subjects had no knowledge of American sign language, they were unable to relate such movements to language or symbolic gestures. The movements, showing the upper limbs and the trunk only, were executed by a human model and were filmed. The video-film was presented on a colour video monitor positioned directly 125 cm in front of the subjects. The 20 movements were devised in five blocks of four movements. Each movement lasted 4 s and was separated from the next one by a 500 ms blank scene. The decision to use delayed imitation on blocks of four movements during the learning phase was made on the basis of the findings of Weeks and colleagues, who demonstrated that learning performance was superior in long-term recall with delayed imitation compared with concurrent imitation, i.e. imitating each movement concurrently with demonstration (Weeks *et al.*, 1996).

Learning procedure

Subjects were requested to carefully observe each block of four actions, and then to reproduce as accurately as possible the movements, irrespective of the order, at the end of the video demonstration. Subjects were provided with feedback and correction on their reproduction throughout the learning phase.

On the first day of learning, each block was presented and then reproduced four times in a row. After each different block, subjects had to recall all movements that they could remember from the preceding block without regard to the order (i.e. 8 movements after 2 blocks, 12 movements after 3 blocks, 16 movements after 4 blocks, and eventually 20 movements after the 5 blocks).

On the second and the third days, subjects were first asked to reproduce as many movements as possible from memory. Then they were shown again each block, as many times as needed, and asked to reproduce the movements. The learning phase was considered over only when the subjects could reproduce 90% of the 20 movements from memory.

Throughout the learning period, subjects' performances were observed and recorded by an experimenter. At the end of the whole learning period, subjects were asked whether they overtly used semantic (verbal) labelling to store or recall

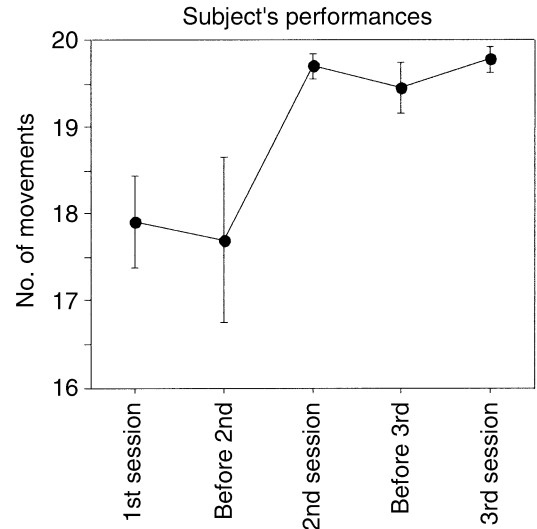


Fig. 1 Subjects' performances across the learning period. The first session corresponds to the first day. Results during sessions correspond to the reproduction of all movements after their observation whereas results before the second and the third sessions correspond to the recall of as many movements as possible from memory. Note the improvement between the first and second day, after which the subjects reached a relative plateau in their performance.

the movements during the acquisition phase. If this were the case, the subject was excluded from the PET session.

Figure 1 illustrates the mean score of reproduction from the nine subjects across the learning sessions. On the final session subjects were able to reproduce 19 or 20 movements from memory. The learning process is demonstrated by a progressive improvement of subjects' performances during all sessions.

PET-activation tasks

Each subject underwent ten separate 60 s scans. There were four experimental conditions and one control condition (Table 1). During each experimental condition, subjects were presented with a video showing an enactment of the meaningless movements, just as in the learning session. Each film comprised five movements repeated three times in a random order (15 stimuli). Each movement lasted 4 s and was separated from the next by a black screen for 500 ms, and each sequence of five actions was separated from the next by a white circle shown for 1 s.

The stimuli were presented on a colour video monitor located in front of the subject at 60 cm from their eyes. The screen was rectangular, and at this distance the display covered the central 19° of the visual field vertically and 26° horizontally. The video apparatus and the subjects were surrounded by a black curtain.

In the control condition, stationary meaningless hand positions were presented. The stimulus structure was similar to that used in experimental conditions, but with no movement. Five meaningless hand positions were used and

Table 1 Five scanning conditions repeated in each subject

Nature of the stimuli	Task instruction	Abbreviation
Stationary hands	Observation without any purpose	S
Learned meaningless movements	Observation without any purpose	LM
Unknown meaningless movements	Observation without any purpose	UM
Learned meaningless movements	Observation to imitate	LMi
Unknown meaningless movements	Observation to imitate	UMi

randomly presented throughout this condition. The aim of this condition was to provide a reference level for experimental conditions.

In two experimental conditions, previously learned meaningless movements were presented. In each video film, the movements presented were arranged such that they did not match the order of appearance used during learning session.

In two other conditions, unknown meaningless movements were presented. These movements had the same features as the learned meaningless movements, but the subjects had never experienced them before.

Experimental design

Each condition was repeated once using different sets of stimuli. The 10 conditions were performed in a counter-balanced order and were separated by a 10 min inter-scan period.

In the control (S) conditions and conditions of observation of learned (LM) or unknown meaningless (UM) movement, subjects were required to carefully observe the stimuli without any specific purpose.

In two other observation conditions of learned (LMi) or unknown (UMi) meaningless movement, subjects were asked to carefully observe the movements in order to imitate them after the scanning period. Subjects were instructed that they would have to accurately reproduce the five movements that they had seen during the scan, regardless of the order of presentation. The subject's performance was recorded on a videotape and then scored on a two-point scale (1, correctly reproduced; 0, unrecognizable or not reproduced).

The subjects were specifically instructed to avoid verbalization during the observation phase as well as during the imitation task. They were also told not to move their hand during the scanning, and this was checked by an experimenter.

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 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.

PET scans were obtained using a Siemens CTI HR+ (63 slices, 15.2-cm axial field of view) PET tomograph with

collimating septa retracted operating in high sensitivity three-dimensional mode. The system had 31 rings which allowed 63 transaxial images to be obtained with a slice thickness of 2.42 mm without a gap in between. A transmission scan, collected with exposure of a ^{68}Ge (333 MBq/pin) ring source, was used to correct for radiation attenuation by the head. A filtered back-projection algorithm was employed for image reconstruction, on a 128×128 matrix (pixel size 2.02 mm, Hanning filter with a cut-off frequency of 0.5 cycles/pixel). rCBF was estimated by recording the distribution of radioactivity following an intravenous bolus injection of 333 MBq of H_2^{15}O through a forearm cannula placed into the brachial vein. The integrated counts collected for 60 s, starting 20 s after the injection time, were used as an index of rCBF. At the beginning of the film, specific instructions were given to focus the subject's attention and to inform 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 time.

PET data analysis

Image analysis was performed on a Silicon Graphics O2 station. The data were analysed with statistical parametric mapping (SPM96 software Wellcome Department of Cognitive Neurology, London, UK) (Friston *et al.*, 1995) implemented in Matlab 4.2 (MathWorks, Natick, Mass., USA). The realigned PET images were spatially normalized into a standard stereotaxic space (Talairach and Tournoux, 1988) using a reference template image (Friston *et al.*, 1995). The resulting voxel dimensions of each reconstructed scan was $2 \times 2 \times 4$ mm in the x , y and z dimension, respectively. The scans were smoothed using a Gaussian filter of 12-mm 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. Regional activations significant at $P < 0.0001$ or $P < 0.001$, uncorrected for multiple comparisons ($Z > 3.72$ or $Z > 3.09$, respectively) were considered. In addition to this standard procedure, and in order to improve the precise anatomical description, the activation foci were superimposed on a reference MRI from one normal subject, available in SPM96. Anatomical identification was performed with reference to the atlases of Talairach and Tournoux and of Duvernoy (Talairach and Tournoux, 1988; Duvernoy, 1991).

Principal component analysis

A single 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 also gives the proportional contribution of that component to the global variance; and (iii) a condition-dependent profile called the 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 from 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 where the contribution is positive are represented by a corresponding positive eigenimage. The same is true for negative images (for a complete description of this analysis, see Friston *et al.*, 1993).

Conjunction analysis

In order to describe the common neural network elicited by the perception of hand movements, whether they have been learned or not, and irrespective of the subject's intention, a conjunction analysis was performed. This analysis was designed such that two or more distinct contrasts each share a common processing difference. The neural correlates of the process of interest are then associated with the common brain regions of activation for each contrast (for a complete description of this analysis, see Price and Friston, 1997). In this experiment, the conjunction analysis between all experimental conditions compared with the control condition [(LMi – S), (UMi – S), (LM – S) and (UM – S)] was performed in order to identify the common network involved in hand movement analysis. In addition, to isolate the regions specifically engaged by learned meaningless, as compared with unknown meaningless actions, and irrespective of the strategy, a conjunction analysis was performed between (LMi – UMi) and (LM – UM).

Main effect

In order to isolate the neural network specifically engaged in the strategy to imitate during the observation, irrespective of the nature of the movements presented, a factorial subtraction was designed: [(LMi + UMi) – (LM + UM)].

Interaction

In order to reveal brain areas where activity is associated with the intention to imitate, which are themselves modulated

by the learning level, an interaction term analysis was performed: [(LMi – LM) – (UMi – UM)].

Results

Performance of subjects

During the imitation tasks, the subjects achieved a score of 90% correct in the reproduction of previously learned movements, and 78% in the recall of unknown movements.

Principal component analysis

Preliminary analysis is given by the principal component analysis which was performed on the whole data set (Fig. 2). This analysis confirmed that the first two components, accounting for 60.2% of the variance, were linked with the experimental design. The first component, which represents 40.2% of the variance, characterizes the intention of the subjects during observation. The positive eigenimage (observation to imitate) engaged the dorsal pathway bilaterally as well as the frontal and the cingulate regions mainly in the right hemisphere. In contrast, the negative eigenimage (observation without any aim) engaged mainly the left frontal and temporal lobes. The second component represents 20% of the variance. The corresponding eigenimages show that activations due to the observation of unknown movements are localized in the posterior part of the brain, whereas observation of learned movements is associated with activations located mainly in the anterior part of the brain.

Areas common to the perception of hand movements

The observation of hand movements, irrespective of the subject's intention, and irrespective of the nature of the stimuli, was associated with bilateral activations in the intraparietal sulcus and in the occipitotemporal junction (V5). Significant activations were found in the superior temporal sulcus, in the middle occipital gyrus, in the posterior cingulate gyrus and in the cerebellum in the right hemisphere; whereas activations were observed in the precuneus (BA 7) and the parieto-occipital fissure in the left hemisphere (Fig. 3; Table 2).

Effect of the learning level

The observation of learned meaningless actions compared with unknown meaningless actions and irrespective of the strategy was associated with bilateral activations located in the inferior parietal lobe (BA 39/7) and in the frontomarginal gyrus (BA 10). Activations were also found in the orbitofrontal gyrus (BA 11) and in the precuneus in the left hemisphere, whereas the anterior cingulate gyrus was found to be activated in the right hemisphere (Fig. 4; Table 3).

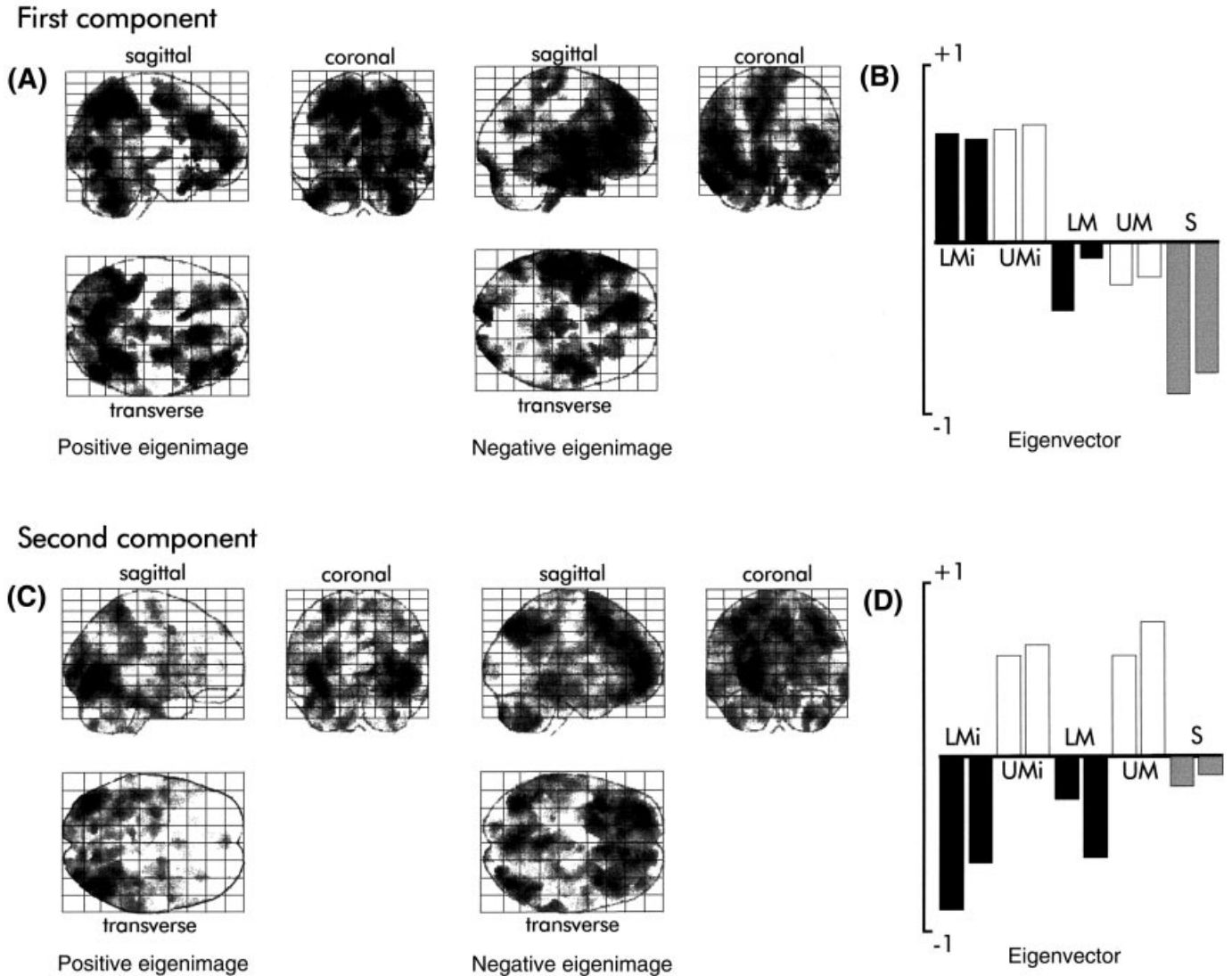


Fig. 2 The first two components of the principal component analysis. The first component accounts for 40.2% of the total variance. (A) Pattern of positive (LMi and UMi, imitation conditions) and negative (LM, UM and S, no purpose conditions) covariance of the first component (eigenimage). (B) Component score across conditions of the first eigenimage (eigenvector). The second component accounts for 20% of the total variance. (C) Pattern of positive (UMi and UM, unknown meaningless actions) and negative (LMi, LM and S, learned meaningless actions and stationary hands) covariance of the second component (eigenimage). (D) Condition-dependent profile of the second component (eigenvector).

Effect of the intention to imitate

Significant activations associated with the intention to imitate, irrespective of the nature of the stimuli [(LMi + UMi) – (LM + UM)] were observed bilaterally in the precuneus (BA 7), in the superior parietal lobule (BA 7) and in the cerebellum. In addition, rCBF increases were found in the inferior parietal lobe (BA 40) and in the anterior cingulate gyrus (BA 32) in the right hemisphere, whereas the cuneus was activated in the left hemisphere. A strong activation was observed in the right dorsolateral prefrontal cortex, which followed the middle frontal sulcus. A similar rCBF response was found in the left hemisphere, but was much less prolonged and less strong. In addition, a bilateral activation was observed in the precentral gyrus (Fig. 5; Table 4).

Interaction between the intention and the learning level

The interaction term [(LMi – LM) – (UMi – UM)] indicates that the orbitofrontal gyrus (BA 11) and the frontomarginal gyrus (BA 10) in the left hemisphere as well as the superior parietal lobule (BA 7) in both sides were associated with the intention to imitate and modulated by the context of learning (Table 5).

Discussion

The present study was designed to demonstrate the effect of visuomotor learning and to assess the modulatory effect of

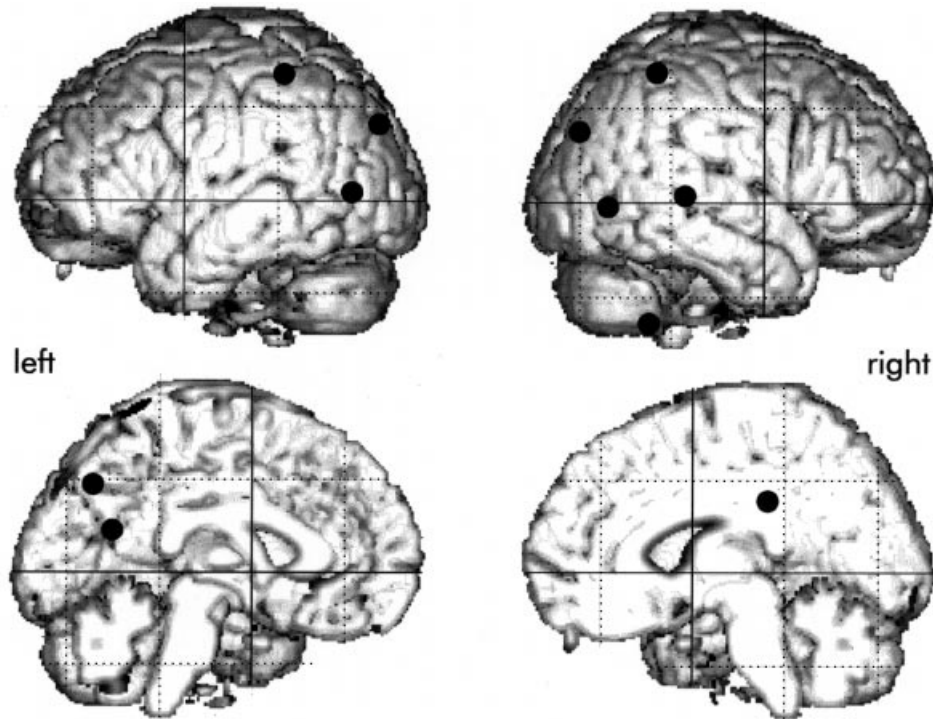


Fig. 3 Areas common to the perception of hand movements. Localization of significant rCBF changes rendered onto lateral (top) and medial (bottom) views of the left and the right hemispheres of a standard template irrespective of the subject’s intention, and irrespective of the nature of the stimuli. Results are listed in Table 2.

Table 2 Areas common to the perception of hand movements

Brain region	Coordinates			Z score
	x	y	z	
L intraparietal sulcus	-32	-42	58	5.37
R intraparietal sulcus	34	-48	56	6.77
L precuneus (BA 7)	-4	-72	42	5.50
L parieto-occipital fissure	-18	-68	34	5.84
L middle occipital gyrus (V3a)	-22	-80	34	4.09
R posterior cingulate	2	-30	28	4.59
R middle occipital gyrus (V3a)	24	-84	28	5.67
L occipitotemporal junction (V5)	-48	-68	8	5.89
R superior temporal sulcus	46	-36	6	4.11
R occipitotemporal junction (V5)	46	-70	0	8.14
R cerebellum	30	-52	-30	4.72

Conjunction between (LMi – S), (UMi – S), (LM – S) and (UM – S). Coordinates are in millimetres, relative to the anterior commissure, corresponding to the Talairach and Tournoux atlas. L/R: left or right hemisphere. Threshold = 3.72 ($P < 0.0001$).

the subject’s intention on the neuronal network involved during the perception of human meaningless actions.

The principal component analysis shows that the greatest amount of the total variance–covariance structure corresponds to our study design: (i) the task demand (i.e. observation to imitate versus observation as such); and (ii) the nature of the actions presented (learned versus unlearned).

Not surprisingly, the common network engaged by the

perception of hand movements during all activation conditions, as revealed by the conjunction analysis, involved the motion complex, which forms a part of the dorsal stream of cortical visual areas, and replicates previous neuroimaging studies (e.g. Zeki *et al.*, 1991; Watson *et al.*, 1993, Dupont *et al.*, 1994; Chawla *et al.*, 1998).

Learning-dependent activity

It is of interest that some areas were found to be modulated by the learning level independent of the subjects’ intention. In particular, the areas located in the occipitotemporal junction (V5/MT) and in the right middle occipital gyrus (V3a), were less activated during the perception of learned meaningless actions as compared to the perception of unknown actions (Fig. 6). This result may be attributed to the attentional demand of the task or to the effect of stimulus familiarity. One possibility is that this increase of activity reflects a top-down effect of implicit attention during the perception of unknown movements. Although the instructions given to the subjects are the same and the differences between the two types of movements are quite small, in one case the movements perceived had been previously learned and in the second case they were new. It is thus conceivable that the covert attention demand is higher for the new movements because of a novelty effect. This is consistent with the role of parietal associations areas in spatial attention (e.g. Haxby *et al.*, 1994). This result can also be explained by a backward

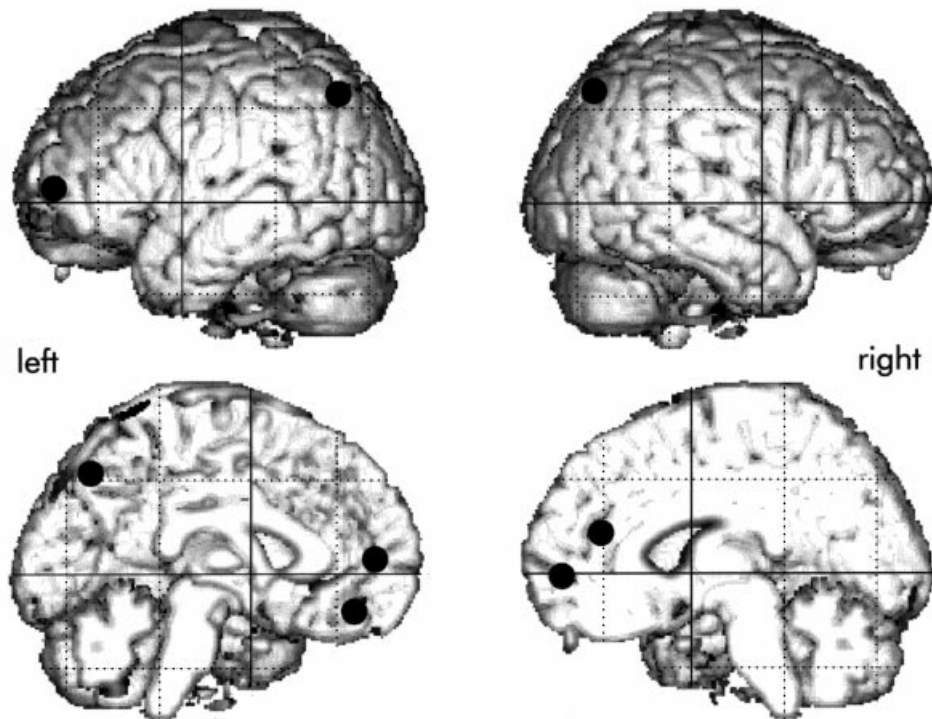


Fig. 4 Effect of the learning. Localization of significant rCBF foci rendered onto lateral (top) and medial (bottom) views of the left and the right hemispheres of a standard template brain during the observation of learned meaningless actions compared with unknown meaningless actions, irrespective of the strategy. Results are listed in Table 3.

Table 3 The effect of the learning level

Brain region	Coordinates			Z score
	x	y	z	
R inferior parietal lobe (BA 39/7)	42	-74	50	5.59
L precuneus (BA 7)	-4	-70	50	5.00
L inferior parietal lobe (BA 39/7)	-38	-68	48	5.38
R cingulate gyrus	16	34	18	5.19
L frontomarginal gyrus (BA 10)	-20	52	4	7.10
R frontomarginal gyrus (BA 10)	14	50	0	4.22
L orbitofrontal gyrus (BA 11)	-22	52	-12	5.42

Brain regions with significantly increased rCBF during observation of learned meaningless actions versus observation of unknown meaningless actions irrespective of strategy (to imitate or without any aim) are given. Conjunction analysis is between (LMi – UMi) and (LM – UM) masked with the two simple contrast with a threshold of $P < 0.005$, $Z > 3.72$.

modulatory effect of the posterior parietal cortex on brain areas relatively early in the visual processing stream (V1, V5) as has recently been demonstrated during attention to visual motion (Büchel *et al.*, 1998).

However, since a difference in rCBF values between perception of learned and unknown movements is also observed during the conditions that required the subjects to watch the movements in order to imitate them, this modification may also be interpreted as reflecting an effect of familiarity. It has been reported that in monkeys' inferior

temporal cortex, the responses of some neurons declined systematically as the novel stimuli became familiar, and then reached a plateau (e.g. Li *et al.*, 1993). The same effect was revealed in a PET study on visual stimuli in the temporal cortex (Vandenberghe *et al.*, 1995). In our study, this decrease was observed in motion-related areas within the dorsal pathway. This is consistent with the fact that subjects perceived hand movements, not pictures or objects. Thus, the reason for reduced cortical activity during the perception of learned movements compared with unknown movements can be due to the fact that the neural populations that represent the familiar stimuli have become more selective through learning.

A second related effect of the familiarity was observed in the cortical areas located bilaterally in the frontopolar area 10, predominantly in the left hemisphere, and in the superior portion of the angular gyrus. These foci are specific to learned actions both for passive observation and observation in order to imitate, and thus are independent of the cognitive strategy but are likely to be driven by the nature of the stimuli.

The meaningless actions that have been subject to visuomotor learning are stored in the long-term memory. The perception of these actions does engage a recognition process, which may correspond to the retrieval of motor memories and to the comparison with the movements visually presented. There is evidence from neuroimaging studies that encoding and retrieval processes in episodic and semantic memories engaged the frontal lobes asymmetrically. Encoding in long-

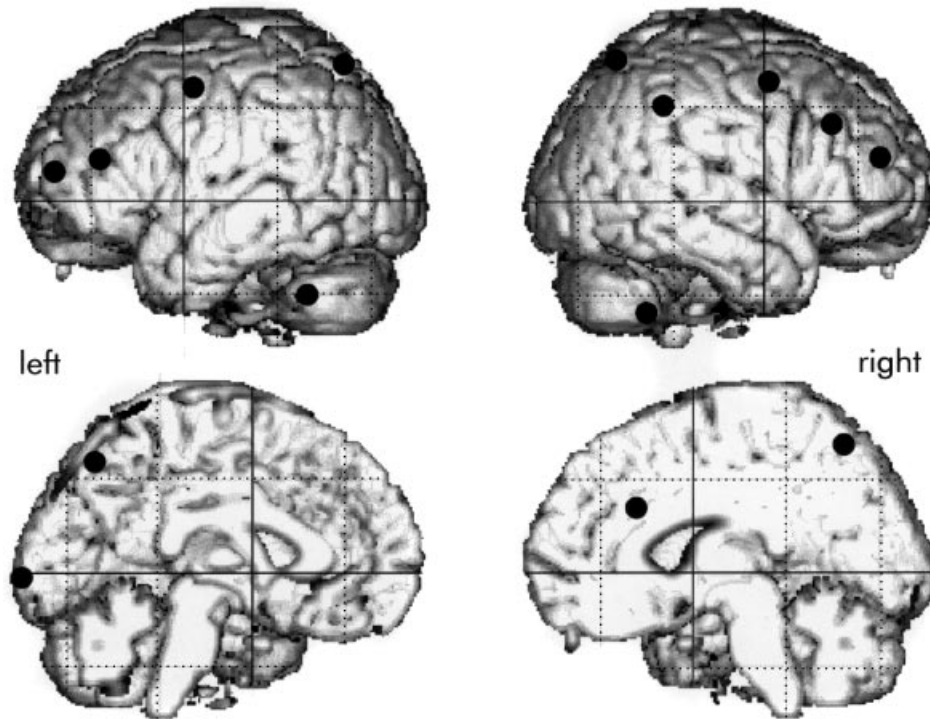


Fig. 5 Effect of the intention to imitate. Localization of significant rCBF foci rendered onto lateral (top) and medial (bottom) views of the left and the right hemispheres of a standard template during the observation of actions with the intent to imitate, compared with the observation without any purpose, and irrespective of the nature of the stimuli. Results are listed in Table 4.

Table 4 The effect of the intention to imitate

Brain region	Coordinates			Z score
	x	y	z	
R superior parietal lobule	24	-64	54	5.69
L precuneus	-8	-74	52	5.23
R precuneus	2	-82	44	4.31
L superior parietal lobule	-16	-66	52	4.83
L precentral gyrus (BA 6)	-30	-4	50	3.78
R precentral gyrus (BA 6)	26	2	50	4.53
R inferior parietal lobe	46	-44	42	5.08
R middle frontal gyrus (BA 9)	44	26	36	5.21
L middle frontal gyrus (BA 9)	-42	26	34	3.25*
R anterior cingulate gyrus	12	24	26	4.85
L middle frontal gyrus (BA 46)	-34	32	22	3.52*
R middle frontal gyrus (BA 46)	32	44	20	4.40
L cuneus	-16	-98	0	4.32
L cerebellum	-32	-52	-38	4.76
R cerebellum	40	-50	-48	4.13

Brain regions with significantly increased rCBF during observation of meaningless actions to imitate versus observation of meaningless actions without any aim (LMi + UMi) – (LM + UM), irrespective of the nature of the movements presented (learned or unknown) are shown. $Z > 3.72$, * $Z > 3.09$.

term memory preferentially activates the left prefrontal cortex, whereas retrieval processing activates the right prefrontal cortex (e.g. Tulving *et al.*, 1994; Buckner and Petersen, 1996). In our study, the activation in the frontopolar cortex was located in the left hemisphere during ‘passive

observation’, and in both hemispheres (but stronger in the left hemisphere) when the aim of the observation was to imitate. The most likely explanation for this apparent discrepancy in terms of lateralization may be the fundamental differences in the nature of the stimuli used. In most of the previous functional imaging studies on encoding and retrieval, episodic and semantic information has been used. In contrast, the present experiment deals with hand movements.

Another influential conceptual framework of the frontal cortex has been proposed by Petrides (Petrides, 1994) (for a recent review, see Rushworth and Owen, 1998). Petrides argued that the ventrolateral frontal cortex constitutes a first level of interaction between modality-specific short- and long-term memory systems, and that it is critical for the active (i.e. explicit) retrieval of information held in posterior cortical regions. In contrast, the dorsolateral prefrontal region (9/46), which receives ventrolateral frontal projections, subserves a second level of interaction of executive process with memory systems when active manipulation of information (planning and monitoring) within working memory is required. This model has been successfully tested with PET by Owen and colleagues, who have also reported an activation in the frontopolar cortex during an externally ordered spatial memory task (Owen *et al.*, 1996). In our study, this region was found to be activated during the perception of learned actions in order to imitate. This is consistent with an active retrieval process of motor memories held in long-term memory for later imitation. However, since

Table 5 The interaction between the intention and the learning level

Brain region	Coordinates			Z score
	x	y	z	
R superior parietal lobule	28	-50	78	3.93
L superior parietal lobule	-20	-52	72	3.69
L frontomarginal gyrus (BA 10)	-24	52	0	3.71
L orbitofrontal cortex	-18	26	-18	3.40

Brain regions where activity is associated with the intent to move that are themselves modulated by the context of learning are shown. Interaction term: (LMi - LM) - (UMi - UM). $Z > 3.09$.

an activation in this region was also found during passive perception of learned actions, which engaged implicit retrieval processing (recognition), we propose that this region not only plays a role in active retrieval, but also in implicit retrieval processing. The bilateral increase in the angular gyrus observed during the perception of learned movements is close to the site of activations that have been reported with a variety of recognition tasks, e.g. using words (Rugg *et al.*, 1998), faces (Haxby *et al.*, 1996) or pictures (Tulving *et al.*, 1996).

This network (i.e. frontal and parietal activations) may thus reflect a common component involved in recognition processing that is relatively independent of the nature of the stimulus material.

Effect of the intention

The major effect of the subjects' intention to imitate was reflected by a strong increase in the dorsal pathway extending to the lateral premotor cortex and to the dorsolateral prefrontal cortex. The activations were bilaterally located but they were much stronger on the right side. In addition, the inferior parietal lobule was activated in the right hemisphere only. At first glance, the prevalence of a right hemisphere dominance might sound contradictory to what is expected. Indeed there is considerable evidence supporting left hemispheric dominance in action selection and action control, as is attested by neuroimaging studies in healthy subjects as well as by clinical observations of apraxic patients following left parietal damage (e.g. Halsband, 1998; Rushworth *et al.*, 1998). However, the predominant activation of the right hemisphere is consistent with the fact that visuospatial processes are preferentially mediated by the right hemisphere (Milner, 1971). In line with this argument are the findings that perceptual neglect generally results from damage to the right inferior parietal lobule (Harvey, 1998). Indeed, several studies have demonstrated that spatial hemineglect in humans, which refers to disorders of spatial cognition, results from damage to the inferior parietal lobe and to the premotor cortex, most often in the right hemisphere (for a recent review, see Vallar, 1998).

The predominance of activations in the right hemisphere

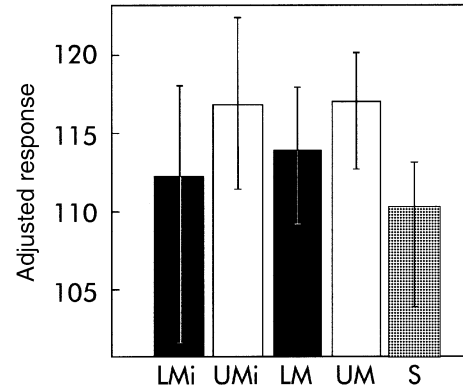


Fig. 6 Learning-dependent activity. The mean rCBF (in arbitrary units adjusted for global flow) and standard deviations from a voxel in the left occipitotemporal junction corresponding to V5 ($x = -46$, $y = -68$, $z = 0$) is shown under the five experimental conditions. Values are plotted at the maximum Z score in this region. Note that this region is less activated during the perception of learned meaningless actions (LMi and LM) than during the perception of unknown meaningless actions (UMi and UM).

are in agreement with a number of other related PET studies performed in the healthy subjects (e.g. Jonides *et al.*, 1993; Jenkins *et al.*, 1994).

The parietal cortex projects heavily to the premotor cortex and to the prefrontal 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 prefrontal cortex (e.g. Petrides and Pandya, 1994). There are several lines of evidence which suggest that the superior parietal lobule is involved in multimodal integration of external information to provide a sensory representation of extrapersonal space. Several PET studies have reported activations in the superior parietal lobule during motor selection with visual cues, based on the integration of spatial information (Deiber *et al.*, 1991; Grafton *et al.*, 1992). Sadato and colleagues suggested that BA 7 may have a role in selecting and monitoring the motor sequence with on-line reference to a working memory in the right premotor cortex (Sadato *et al.*, 1996). Finally, the activation in the mid-dorsal part of the lateral frontal cortex (BA 9 and 46) is in agreement with previous studies concerning the planning of voluntary actions (Frith *et al.*, 1991; Jahanshahi and Frith, 1998) and on-line manipulation of spatial information within the working memory (Owen *et al.*, 1996). Therefore, parietal activations may reflect visual attention and integration of visually presented movements for visuomotor transformations. Joint activations of parietal areas with premotor and prefrontal cortex which occur during observation to imitate would thus account for the transfer of the processing of movement patterns into motor plans within the working memory. This hypothesis is in line with Fuster's suggestion that the prefrontal cortex by functional linkage with the posterior cortex plays a key role in the processing needed for prospective action (Fuster, 1997). It is also in agreement with the work of Goldenberg and Hagmann, who proposed

from clinical examination of apraxic patients that the imitation of meaningless gestures involves an intermediate step that requires the elaboration of a motor representation (Goldenberg and Hagmann, 1997).

The orbitofrontal cortex was engaged in the left hemisphere during the perception of learned actions both during passive observation and to a much greater extent during perception for later imitation. This finding is in line with the inhibitory role of the orbitofrontal cortex in action planning. The above hypothesis is based on clinical observation and recent imaging studies in the healthy subjects. Patients with lesions of this part of the frontal cortex can exhibit an exaggerated dependence on environmental cues, which has been interpreted by Lhermitte and colleagues to be a consequence of impaired inhibition of automatic, externally triggered actions (Lhermitte *et al.*, 1986). Further evidence in support of this hypothesis has been reported by Marshall and colleagues from a PET study performed in a single case of left-sided hysterical paralysis (Marshall *et al.*, 1997). The requirement to move the paralysed leg was correlated with a significant activation in the right orbitofrontal cortex. Activation of the orbitofrontal cortex has been reported in a previous PET study during the observation of meaningful actions in order to imitate (Decety *et al.*, 1997); the authors suggested that this region may have an inhibitory role on the action to be performed.

Conclusion

Our study has demonstrated that both visuomotor learning and intention have a modulatory effect on the neural network engaged by the perception of movements. The learning level (familiarity) is reflected both by a reduction in activity within the motion complex and by an increase within the inferior parietal cortex and in the frontopolar cortex. The subject's strategy to imitate is associated with the involvement of several cortical regions (parietal and prefrontal) that are interpreted as an effect of intention to action. Finally, no neural activity in the ventral premotor cortex, which is usually interpreted as a key structure in the action recognition process, was found in this study. We suggest that this latter region might merely be associated with implicit semantic processing.

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