Brain (1996), **119**, 593–609

Action recognition in the premotor cortex

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Summary

We recorded electrical activity from 532 neurons in the rostral part of inferior area 6 (area F5) of two macaque monkeys. Previous data had shown that neurons of this area discharge during goal-directed hand and mouth movements. We describe here the properties of a newly discovered set of F5 neurons ('mirror neurons', n = *92) all of which became active both when the monkey performed a given action and when it observed a similar action performed by the experimenter. Mirror neurons, in order to be visually triggered, required an interaction between the agent of the action and the object of it. The sight of the agent alone or of the object alone (three-dimensional objects, food) were ineffective. Hand and the mouth were by far the most effective agents. The actions most represented among those activating mirror neurons were grasping, manipulating and placing. In most mirror neurons (92%) there was a clear relation between the visual action they responded to and the motor response they coded. In ~30% of mirror neurons the congruence was very strict and the effective observed and executed actions corresponded both in terms of general action (e.g. grasping) and in terms of the way in which that action was executed (e.g. precision grip). We conclude by proposing that mirror neurons form a system for matching observation and execution of motor actions. We discuss the possible role of this system in action recognition and, given the proposed homology between F5 and human Brocca's region, we posit that a matching system, similar to that of mirror neurons exists in humans and could be involved in recognition of actions as well as phonetic gestures.*

Keywords: action encoding; visual responses; premotor cortex; macaque monkey

Introduction

Classically, the agranular cortex of the primate frontal lobe was subdivided into two large cytoarchitectonic areas: area 4, containing giant pyramidal cells, and area 6, almost completely devoid of them (Brodmann, 1909). To this simple anatomical subdivision corresponded an equally simple functional parcellation. Two main motor areas were delimited. The 'primary motor area' formed by area 4 and most of the area 6 located on the lateral brain convexity, and the 'supplementary motor area', formed by the sector of area 6 that is located on the mesial brain surface. The remaining part of area 6 formed (at least according to some authors) a third motor area defined as the 'premotor area' (Fulton, 1935).

Modern studies of the agranular frontal cortex radically modified this picture. New data on cytoarchitectonics (Barbas and Pandya, 1987; Matelli *et al.*, 1991), histochemistry (Matelli *et al.*, 1985), neurochemistry (Zilles *et al.*, 1995, 1996) and hodology (Matsumura and Kubota, 1979; Muakkassa and Strick, 1979; Matelli *et al.*, 1986; Dum and Strick, 1991; Kurata, 1991; He *et al.*, 1993; Galea and Darian Smith, 1994) of the agranular frontal region showed that the agranular frontal cortex, rather than being constituted of two cytoarchitectonic areas, is formed by a mosaic of areas with distinctive differences in structure and connectivity. Physiological studies (Gentilucci *et al.*, 1988; Rizzolatti *et al.*, 1988; di Pellegrino and Wise, 1991; Mushiake *et al.*, 1991; Kurata and Hoffman, 1994) provided convincing evidence that different motor functions correspond to these structural differences. Finally, in contrast to the classical notion that the premotor cortex essentially controls synergic axio-proximal movements (*see* Humphrey, 1979), recent behavioural and single neuron studies showed that premotor cortex is involved also in 'cognitive' functions. It plays a role in coding space (Gentilucci *et al.*, 1983, 1988; Rizzolatti *et al.*, 1983; Fogassi *et al.*, 1992; Graziano and Gross, 1994; Graziano *et al.*, 1994), in extracting the intrinsic properties of the objects (Rizzolatti *et al.*, 1988; Jeannerod *et al.*, 1995), as well as in associative learning (Halsband and Passingham, 1985; Petrides, 1985; Passingham, 1988, 1993; Mitz *et al.*, 1991).

Among the various agranular frontal areas one of particular interest for its complex functions is F5 (Matelli *et al.*, 1985). In the monkey this area lies immediately caudal to the inferior arm of the arcuate sulcus. Stimulation and recording experiments showed that F5 is concerned with both hand and mouth movements (Kurata and Tanji, 1986; Gentilucci *et al.*, 1988; Rizzolatti *et al.*, 1988; Hepp-Reymond *et al.*, 1994). Hand movements are represented mostly in its dorsal part, while mouth movements tend to be represented ventrally.

Whereas little is known about the functional properties of 'mouth' neurons, the properties of 'hand' neurons were extensively studied. 'Hand' neurons discharge during specific goal-related movements such as grasping, tearing, manipulating and holding. Many of them are specific for a particular type of hand movement, discharging exclusively during certain types of hand grip (e.g. precision grip or finger prehension) (Rizzolatti *et al.*, 1988). In addition, a set of F5 neurons becomes active at the presentation of three-dimensional objects, in the absence of any overt movement. In many cases these visually triggered discharges are present only if the size of the presented object is congruent with the type of grip coded by the neuron (*see* Jeannerod *et al.*, 1995).

Recently, we discovered a particular set of F5 neurons, which discharged both during monkey's active movements and when the monkey observed meaningful hand movements made by the experimenter. Frequently there was a clear similarity between the effective observed movement and the effective executed movement (di Pellegrino *et al.*, 1992). The aim of the present article is to give a detailed description of the properties of these 'mirror' neurons. The possible clinical implications of these findings will be discussed.

Methods

Electrical activity from single neurons was recorded from the rostral part of inferior area 6 (sector F5, Matelli *et al.*, 1985) in two monkeys (*Macaca nemestrina*). In the first monkey (MK8) activity from neurons in the left and right hemispheres was recorded and in the second one (MK9) recordings were made from neurons in the left hemisphere only. All experimental protocols were approved by the Veterinarian Animal Care and Use Committee of the University of Parma and complied with the European law on the humane care and use of laboratory animals.

Neuron testing and behavioural paradigm

Once a neuron was isolated, its visual and motor properties were first tested as we demonstrated (Rizzolatti *et al.*, 1988, 1990). Briefly, the monkey, seated on a primate chair, was presented with a variety of objects. These consisted of food items (e.g. raisins, pieces of apple, sunflower seeds) and objects at hand in the laboratory. The objects were presented within and outside the reaching distance of the monkey. The monkey was trained to fixate the objects and, when they were moved toward it, to reach and grasp them.

Grasping was studied by presenting objects of different size and shape and recording the evoked movements on a videotape. Objects of different size evoked different types of prehensions. The most common were as follows. (i) 'Precision grip', i.e. opposition of the index finger and thumb. This grip was evoked by small objects. (ii) 'Finger prehension', i.e. opposition of the thumb to the other fingers. The monkeys used finger prehension to pick up middle-size objects from a deep narrow container. (iii) 'Whole hand prehension', i.e. flexion of all fingers around an object. It was evoked by large objects. Reaching was studied by presenting various objects in the four quadrants of the visual space and by repeating over and over the presentations. By examining a large variety of proximal–distal movement combinations, it was usually possible to assess which proximal or distal movement was effective in triggering a given neuron. For discussion of this testing method *see* Rizzolatti *et al.* (1988).

Some neurons were further studied by using a testing box placed in front of the monkey. The front door of the box was formed by a one-way mirror which, during the intertrial periods, prevented the monkey from seeing inside the box. Geometric solids (spheres and cylinders) of different sizes were used as stimuli. Each of them was placed inside the box in separate series of blocked trials. The monkey started each trial by pressing a switch with the thumb and the index finger. Pressing the switch lit the box and made the object visible. After a delay of 1.2–1.5 s, the door opened, allowing the monkey to reach for the object. The animal was rewarded with a piece of food placed in a well under the object. If the monkey released the switch before the door opened, the trial was aborted. Some neurons were also tested in complete darkness; the light of the testing box was turned off before the door opening and the monkey grasped the object with no visual guidance.

Testing of 'complex' visual properties

In addition, all recorded neurons were studied by examining their discharge while one experimenter performed a series of motor actions in front of the monkey. These actions were related to food grasping (presenting the food to the monkey, putting it on a surface, grasping it, giving it to a second experimenter or taking it away from him), to food manipulation, and to grasping and manipulation of other objects. Furthermore, gestures with or without emotional content were made in front of the animal (lifting the arms, waving the hands, threatening the monkey, displaying unpleasant objects).

In order to verify whether the recorded neuron coded specifically hand–object interactions, the following actions were also performed: movements of the hand mimicking grasping in the absence of the object; prehension movements of food or other objects performed with tools (e.g. forceps, pliers); simultaneous combined movements of the food and hand, spatially separated one from the other. All experimenter's actions were repeated on the right and on the left of the monkey at various distances.

Physiological procedures and data recording

The surgical procedures for the construction of the head implant were the same as described in previous studies (for details, *see* Gentilucci *et al.*, 1988; Rizzolatti *et al.*, 1990). The head implant included a head holder and a chamber for single-unit recordings. After surgery, monkeys were monitored until they were fully awake, given ketorolac (0.5 mg kg^{-1} i.m., twice) for analgaesia, and returned to their home cage. Monkeys were given 1–2 weeks for recovery before the start of the experiments.

Single neurons were recorded using tungsten microelectrodes (impedance 0.5–1.5 MΩ, measured at 1 kHz) inserted through the dura. Neuronal activity was amplified and monitored with an oscilloscope. Individual action potentials were isolated with a time–amplitude voltage discriminator (BAK Electronics, Germantown, Md, USA). The output signal from the voltage discriminator was monitored and fed to a PC for analysis.

The animal's behaviour and the experimenters' actions during testing of complex visual properties were recorded on one track of a videotape. The neural activity was simultaneously recorded on a second track, in order to correlate the monkey's behaviour or the experimenters' actions to the neuron's discharge. For most neurons, histograms of visual and motor responses were constructed. By using a contact detecting circuit, a signal was sent to a PC whenever the monkey or the experimenter touched a metal surface with their hands. This signal allowed the alignment of the histograms with the moment in which the motor action performed either by the experimenter or by the monkey was concluded. Response histograms were constructed by summing eight to 10 individual trials.

The recording microelectrodes were also used for electrical intracortical microstimulation (train duration, 50 ms; pulse duration, 0.2 ms; frequency, 330 Hz; current intensity, 3–40 μA). The current strength was controlled on an oscilloscope by measuring the voltage drop across a 10 kΩ resistor in series with the stimulating electrode.

EMG activity was recorded bipolarly using surface electrodes. The activity was band-pass filtered (10–800 Hz), A/D converted and stored on a PC for successive analysis. The recorded muscles were orbicularis oris, flexor digitorum superficialis, extensor digitorum communis and opponens pollicis. The EMG recordings were made in special sessions in which all testing procedures were the same as those used in sessions in which neurons were recorded.

Histological identification

About 1 week before killing the monkey, a series of small electrolytic lesions (10 μA cathodal current for 10 s), equally spaced one from another, were made to delimit the border of the studied area. After the last experiment the animal was anaesthetized with ketamine (15 mg kg^{-1}, i.m.) and, after an additional dose of sodium thiopental (30–40 mg, i.v.), perfused through the left ventricle with warm buffered saline followed by fixative (for details, *see* Matelli *et al.*, 1985). The animal was then placed in the stereotactic apparatus, the dura was removed and the stereotactic coordinates of the arcuate and central sulci were assessed. The brain was blocked coronally on a stereotactic frame, removed from the skull, photographed, and then frozen and cut coronally (each section 60 μm). Alternate sections were stained with the Nissl method and reacted for cytochrome oxidase histochemistry. The locations of the penetrations were reconstructed and related to the various cytochrome oxidase areas of the frontal agranular cortex (Matelli *et al.*, 1985).

Results

The activity of 532 neurons was recorded from area F5. Ninety-two of them discharged both when the monkey made active movements and when it observed specific meaningful actions performed by the experimenter. We will refer to these neurons as 'mirror neurons'. Their visual and motor properties will be described in the next paragraphs.

Visual properties of mirror neurons

The visual stimuli most effective in triggering mirror neurons were actions in which the experimenter's hand or mouth interacted with objects. The responses evoked by these stimuli were highly consistent and did not habituate. The presentation of common visual objects, including interesting stimuli such as food items, sight of faces or body movements were ineffective. Similarly, actions made using tools, even when very similar to those made using hands, either did not activate the neurons or activated them only very weakly. Gestures having emotional meaning were also ineffective. The distance from the monkey at which the effective observed action was made did not influence the response intensity.

The observed hand actions which most frequently activated the mirror neurons were grasping, placing and manipulating. Out of 92 mirror neurons triggered by the observation of hand movements, 51 were active only during the observation of a single action. Thirty-eight neurons were activated by two or three of them. Three neurons discharged when the monkey observed the experimenter grasping food with his hand or his mouth. Table 1 shows the hand actions effective in activating the neurons and the number of mirror neurons activated by each of them. It is important to note that only the actions listed in Table 1 (among the many tested, *see* Methods) were effective in triggering the neurons.

Types of mirror neurons

As described above, the majority of mirror neurons responded to the observation of one action only. In this section we will show examples of these neurons and illustrate their properties. For the sake of simplicity the different types of neurons will be named with the action that activated them. The terms 'grasping neurons', 'manipulating neurons', 'holding neurons', etc. will be used only for descriptive purposes and are neutral as far as their function is concerned. The properties of neurons responding to two or more actions were the same

Table 1 *Mirror neurons subdivided according to hand actions effective in activating them*

Observed hand actions	No. of neurons
Grasping	30
Placing	7
Manipulating	7
Hands interaction	5
Holding	2
Grasping/placing	20
Grasping/manipulating	3
Grasping/hands interaction	3
Grasping/holding	5
Grasping/grasping with the mouth	3
Placing/holding	1
Hands interaction/holding	1
Grasping/placing/manipulating	1
Grasping/placing/holding	4
Total	92

as those responsive to one action, but for their lower degree of specificity. Examples of grasping/manipulating or grasping/placing neurons will not be presented for reason of space.

Grasping neurons

Those neurons that discharged in response to the sight of a hand approaching and grasping an object, we named 'grasping' mirror neurons. Some grasping mirror neurons stopped firing almost immediately as the hand grabbed the object, others continued to discharge for a while after the end of the action.

An example of a grasping mirror neuron is shown in Fig. 1. Each trial started with the stimulus presentation (a raisin placed on a tray). No discharge was present. In Fig. 1A, the stimulus was grasped by the experimenter. The neuron's discharge began during hand shaping and continued until the hand left the stimulus. No response was present during the phase subsequent to the grip when the tray with the food was moved toward the monkey. The neuron fired again when the monkey grasped the food. In Fig. 1B, the same stimulus was grasped using a tool. In this condition only a weak discharge was elicited by action observation.

Another example of a grasping mirror neuron is shown in Fig. 2. This neuron belonged to a subset of neurons ($n = 18$) that were selective not only to the grasping movement but also to the way in which grasping was executed (e.g. precision grip, finger prehension, whole hand prehension). In Fig. 2A, the monkey observed the experimenter taking a small piece of food, held on the tip of a stylus, using a precision grip. There was a strong discharge which initiated with the onset of the hand movement. The specificity of the visual response is shown in Fig. 2B. Here the experimenter also grasped an object (a syringe filled with apple juice), but using a whole-hand prehension. No response was present. In Fig. 2C the monkey observed the experimenter mimicking the same

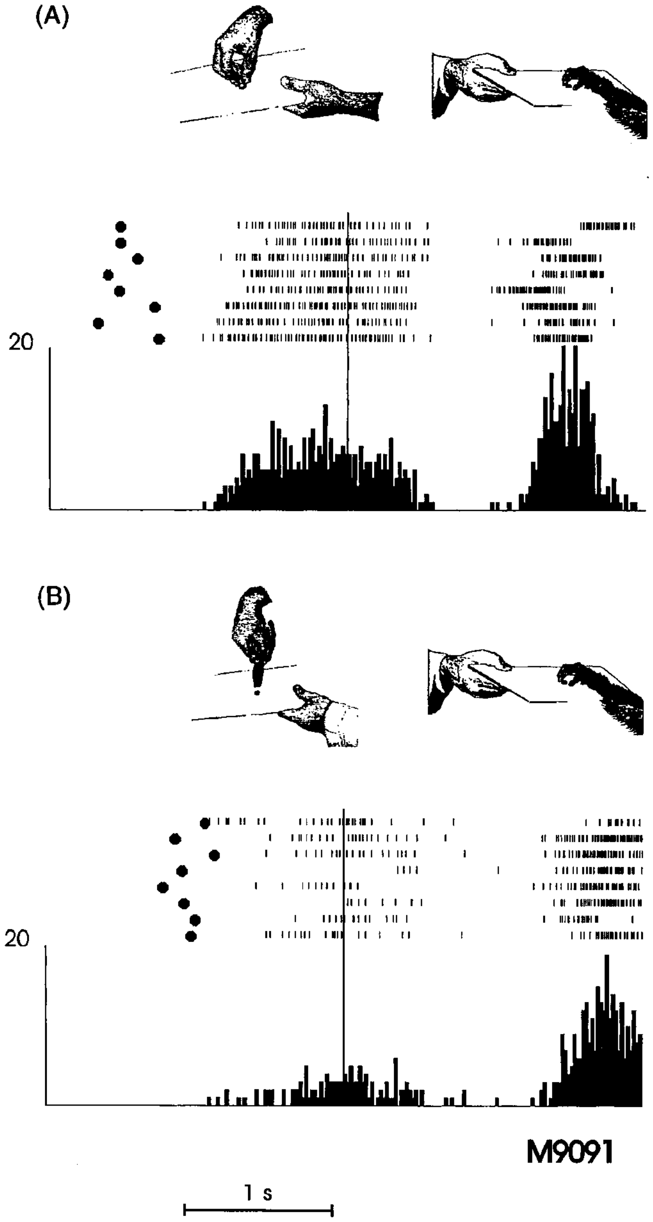

Fig. 1 Visual and motor responses of a grasping mirror neuron. The behavioural conditions are schematically represented in the upper part of each panel. In the lower part are shown a series of eight consecutive trials (raster display) and the relative response histogram. (**A**) A tray with a piece of food was presented to the monkey, the experimenter made the grasping movement toward the food and then moved the food and the tray toward the monkey who grasped it. The phases when the food was presented and when it was moved toward the monkey were characterized by the absence of neuronal discharge. In contrast, a strong activation was present during grasping movements of both the experimenter and the monkey. (**B**) As above, except that the experimenter grasped the food with pliers. In both **A** and **B**, rasters and histograms are aligned with the moment at which the experimenter touched the food either with his hand or with the pliers (vertical line). Filled circles indicate the beginning of the trials. Histograms bin width = 20 ms. Ordinates, spikes/bin; abscissae, time.

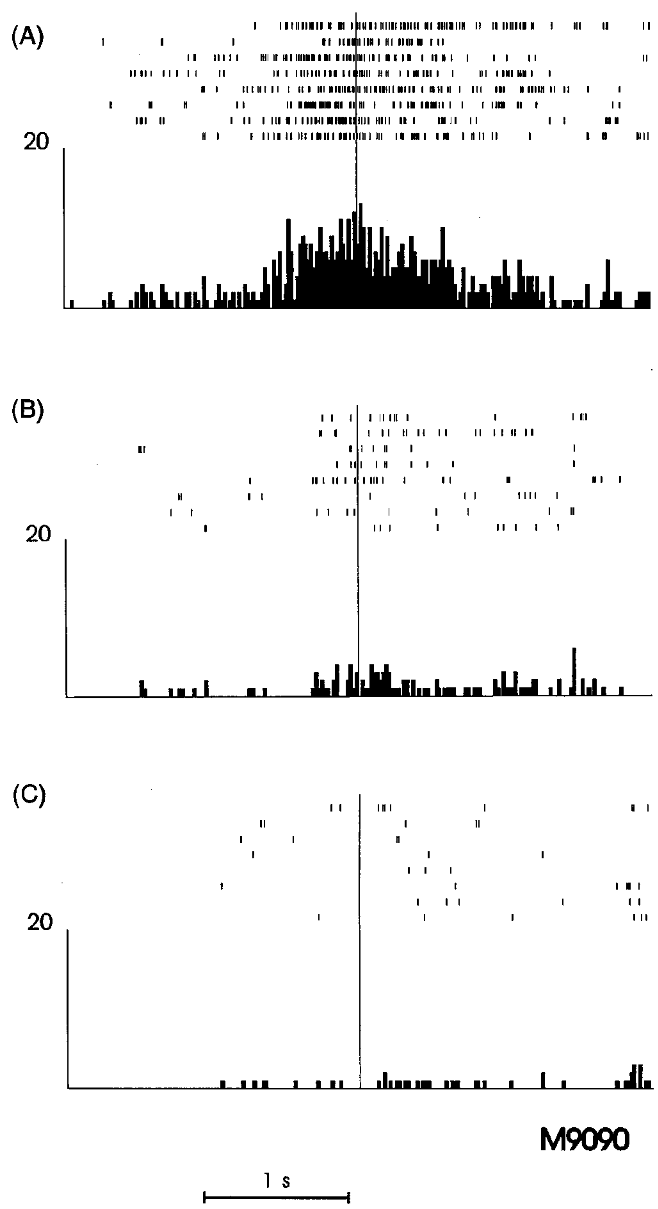

Fig. 2 Visual responses of a grasping mirror neuron: (**A**) precision grip—the experimenter grasped a piece of food held on the tip of a stylus; (**B**) whole hand prehension—the experimenter grasped a syringe filled with apple juice; (**C**) the experimenter mimicked a precision grip in the absence of the object. Conventions as in Fig. 1.

precision grip that triggered the neuron in Fig. 2A, but the movement was made in the absence of the object. No response was present.

Placing neurons

Those neurons that discharged when the experimenter moved a stimulus toward a plane or a support, we named 'placing' mirror neurons.

Figure 3 illustrates an example of a placing neuron. In Fig. 3A, an empty tray was presented to the monkey at the beginning of each trial. The experimenter then placed a piece of food on it. The discharge started with the hand placing movement and ceased when the hand moved away from the food. In Fig. 3B the same tray was presented to the monkey, but with a piece of food located on it. The experimenter then grasped the food. The evoked discharge was much weaker than in Fig. 3A.

Manipulating neurons

Those neurons that responded when the experimenter touched and moved an object with his fingers in order to take possession of it, we defined as 'manipulating' mirror neurons.

Figure 4 shows an example of a manipulating neuron. In Fig. 4A, the monkey observed the experimenter taking out a raisin from a well in a tray using his index finger. Each trial started with the presentation of the tray. The discharge began just before the experimenter's finger touched the food, and ceased when the food was retrieved from the hole. In Fig. 4B, the experimenter mimicked the movement performed in Fig. 4A, but without an object. The neuron was only very weakly activated. In Fig. 4C, the experimenter retrieved the stimulus with a tool. No response was evoked.

Hands interaction neurons

Those neurons that responded best to the movement of one hand toward the other which was holding an object, we called 'hands interaction' mirror neurons. An example of a neuron of this type is shown in Fig. 5. In Fig. 5A, the monkey observed the experimenter moving his hand with food towards the other hand. The discharge began with the movement onset and virtually ceased when the two hands touched each other and the hand holding the food began to move back to its initial position. In Fig. 5B, the monkey observed the experimenter making the same movement as in Fig. 5A, but without food. In Fig. 5C, the experimenter held in each hand a disc attached to a long handle. One disc was held stationary, while the other was moved in a trajectory similar to that of the moving hand in Fig. 5A and B. Note the progressive discharge decrease from A to C in Fig. 5. No response was evoked when the monkey observed the experimenter grasping food or other objects (trials not shown in the Fig. 5).

Holding neurons

Those neurons that were activated when the monkey observed an object kept in the hand of the experimenter, we called 'holding' mirror neurons. The discharge ceased as soon as the experimenter moved his hand away from the food. Except for two neurons, neurons responding to the observation of a hand holding an object responded also to the observation of other actions.

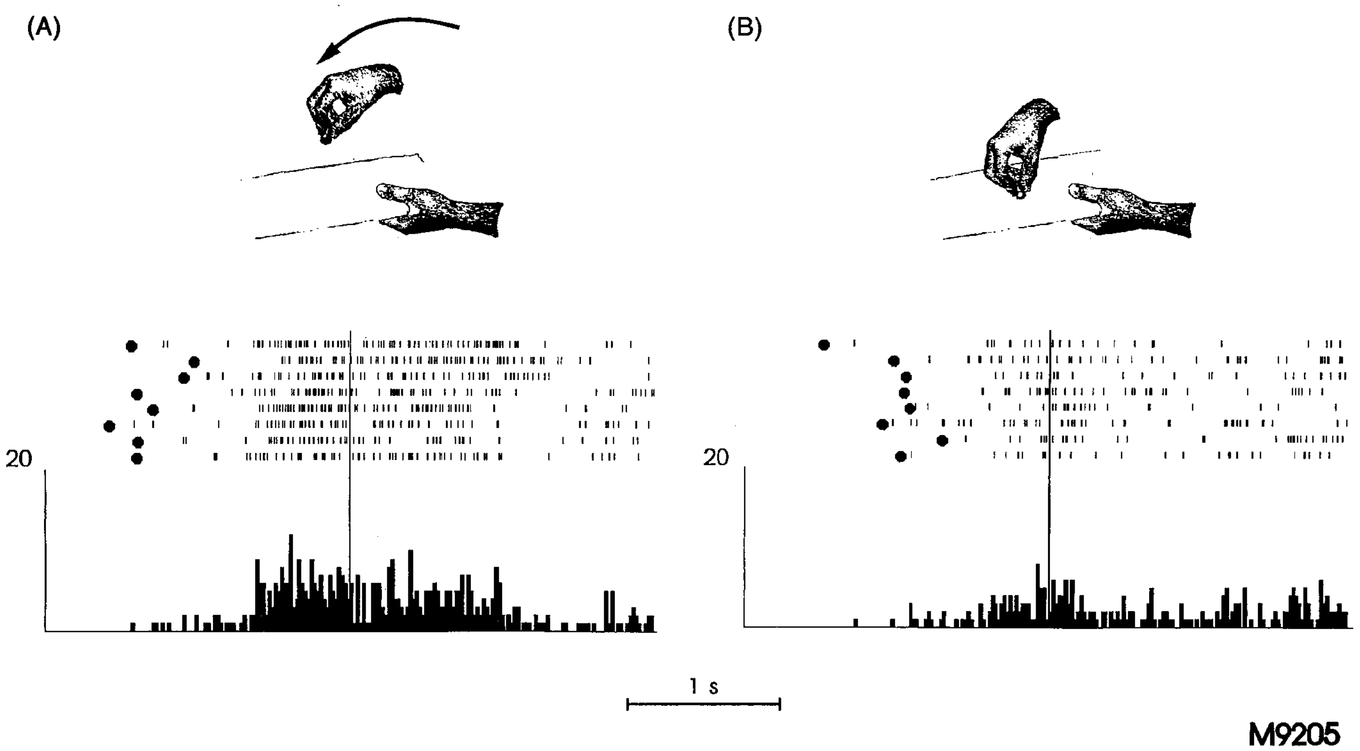

Fig. 3 Visual responses of a placing mirror neuron. (A) The experimenter placed a piece of food on a tray. Rasters are aligned with the moment at which the experimenter's hand touched the tray surface. The neuron's discharge started when the hand approached the tray and continued for the whole time the hand was in contact with the food. (B) The experimenter grasped a piece of food located on a tray. A tray was presented to the monkey with a piece of food on it, the experimenter moved his hand toward the food and grasped it. As in A, the rasters are aligned with the moment at which the experimenter's hand touched the tray surface. The responses during grasping observation were much weaker than during placing observation. Conventions as in Fig. 1.

Mirror-like neurons

Twenty-five neurons responded to the observation of hand actions but, unlike mirror neurons, lacked motor properties. Table 2 illustrates the different types of 'mirror-like' neurons classified according to the hand actions effective in triggering them. One neuron responded to the observation of mouth and hand grasping movements.

Other visual characteristics of mirror and mirror-like neurons

The response of some mirror and mirror-like neurons depended, in addition to the type of the observed action, on other action-related factors. These factors included the hand used by the experimenter and the action direction.

Hand preference

Thirty-two neurons were tested using the right and the left hand, alternately. The action was performed first in front of the monkey, and then on its left and right. In 12 neurons (37.5%), the discharge was markedly influenced by the hand used. Nine neurons responded more strongly when the experimenter used the hand ipsilateral to the monkey's recorded hemisphere (i.e. the experimenter's left hand when the recorded hemisphere was the left one and the experimenter's right hand when the recorded hemisphere was the right one), three preferred the contralateral hand. In absolute terms five neurons preferred the right hand and seven the left hand.

An example of a hand-selective mirror neuron is illustrated in Fig. 6. This neuron discharged strongly only when the experimenter held food with his left hand (Fig. 6A1, B1 and C1). The same hand preference was found when the effective action was made centrally (Fig. 6A), on the left (Fig. 6B) or on the right (Fig. 6C) of the monkey. A hand preference was observed also during the monkey's active grasping movements (Fig. 6D). The preferred hand during active movements was, however, the right hand (Fig. 6D1), i.e. the hand opposite to that evoking the best visual responses. Note that in the case of face to face stance, the hand of an acting individual corresponds spatially to the opposite hand of the observing individual.

Action direction

Cell preference for the direction of the observed action was tested in 47 mirror neurons. The experimenter, standing in front of the monkey, repeated the same action performing it alternately from left to right and from right to left. Thirty

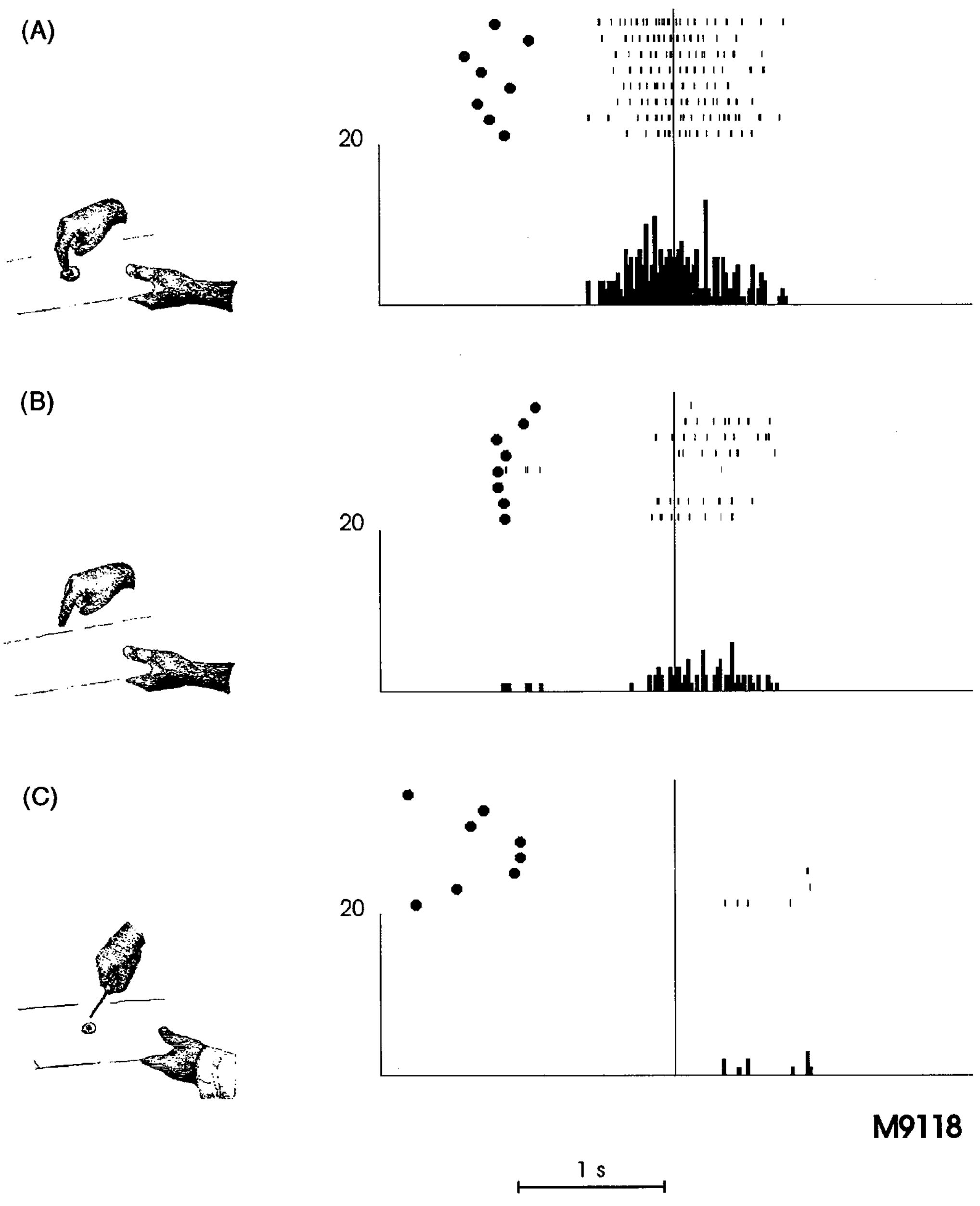

Fig. 4 Visual responses of a manipulating mirror neuron. (**A**) The experimenter retrieved a piece of food placed in a well in a tray, using his index finger. This was the only action that activated the neuron. (**B**) The same action was mimed without food. (**C**) the food was retrieved using a tool. Conventions as in Fig. 1.

neurons showed directional preference. The great majority of them (83.3%) preferred the direction toward the recorded side (e.g. from right to left for neurons recorded from the left hemisphere). The preference remained constant, regardless of whether the action was made in the right hemispace, left hemispace or centrally.

Figure 7 shows an example of a directionally selective grasping mirror neuron. The neuron discharged more strongly when the experimenter's reaching–grasping action was executed toward the left (recorded) side (Fig. 7A1, B1 and C1) than toward the right side (Fig. 7A2, B2 and C2). The direction preference was more pronounced when the action was performed centrally or in the monkey left space (Fig. 7A and B) than when it was performed in the right space (Fig. 7C).

Motor responses of mirror neurons

As previously described (for review, *see* Jeannerod *et al.*, 1995) typically F5 neurons discharge selectively during specific goal-directed motor actions. The motor properties of mirror neurons studied in the present experiment were undistinguishable from those of other F5 neurons. They also showed a clear specificity for particular motor acts. Table 3

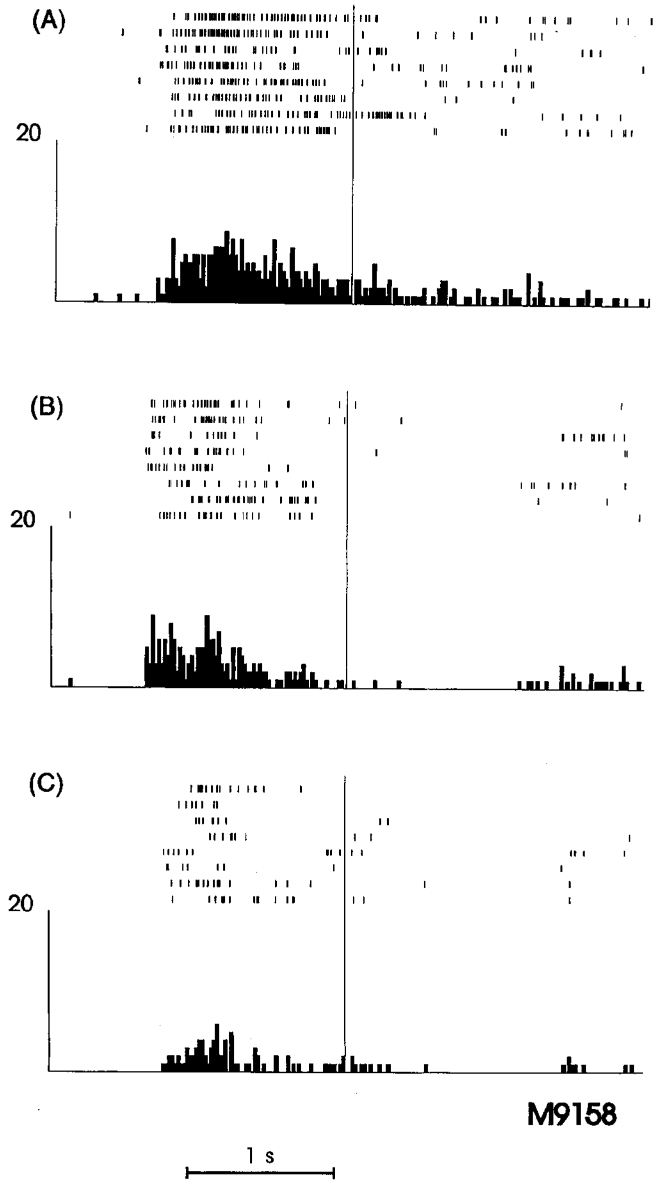

Fig. 5 Visual responses of a mirror neuron responding to interaction between the hands. (**A**) The experimenter moved one hand holding a piece of food toward the other hand. (**B**) Same movement as in **A**, but without food. (**C**) The experimenter held in each hand a disc attached to a long handle. One disc was held stationary, while the other was moved in the same way as the moving hand in **A** and **B**. Rasters are aligned with the moment at which hands (**A** and **B**) or discs (**C**) touched one another. For other conventions see Fig. 1.

shows the motor acts effective in activating them. The classification adopted here is that previously used by Rizzolatti *et al.* (1988) for classifying the motor responses of F5 neurons. 'Grasping-with-the-hand-and-the-mouth' cells were neurons that discharged regardless of whether the motor act was performed using the hand or the mouth. As in the case of non-mirror F5 neurons of the same class, 'grasping-with-the-hand-and-the-mouth' were, with only two exceptions, unselective for particular types of grip.

Table 2 *Mirror-like neurons subdivided according to hand actions effective in activating them*

Observed hand actions	No. of neurons
Grasping	7
Placing	3
Hands interaction	6
Holding	1
Grasping/placing	4
Grasping/hands interaction	2
Grasping/grasping with the mouth	1
Manipulating/hands interaction	1
Total	92

'Grasping-with-the-hand' neurons responded only to grasping movements made with the hand. As for the non-mirror F5 neurons (Rizzolatti *et al.*, 1988), 'grasping-with-the-hand' neurons formed the largest motor class ($n = 60$). Among them, 38 were not selective, while 22 preferred a specific type of prehension. Eleven of them discharged during precision grip, seven during finger prehension, two during whole hand prehension. Two neurons responded both to precision grip and finger prehension.

Finally, neurons responding to proximal arm movements were very rare ($n = 2$). They both fired in association to arm movements directed towards the mouth.

Action observation versus action execution

Mirror neurons are characterized by two main properties: responsiveness to the sight of meaningful actions and activation with active movements. These two properties are not easily dissociable because usually, when the monkey interacts with an object, it also sees its own movements. Thus the discharge recorded during the monkey's actions could reflect the neuron's visual properties, its motor properties, or both. In order to control for this possibility a series of mirror neurons were studied while the monkey executed the most effective motor action in light and dark. The results showed that all tested neurons ($n = 14$) fired in both these conditions. Informal testing of the other neurons was consistent with this result. The responses of two neurons tested with and without hand vision are shown in Fig. 8.

Relationship between visual and motor responses of mirror neurons

Visuo-motor congruence

In most mirror neurons there was a clear relationship between the visual action they responded to and the motor response they coded. Using as classification criterion the congruence between the effective observed action and the effective executed action, we partitioned the mirror neurons into three

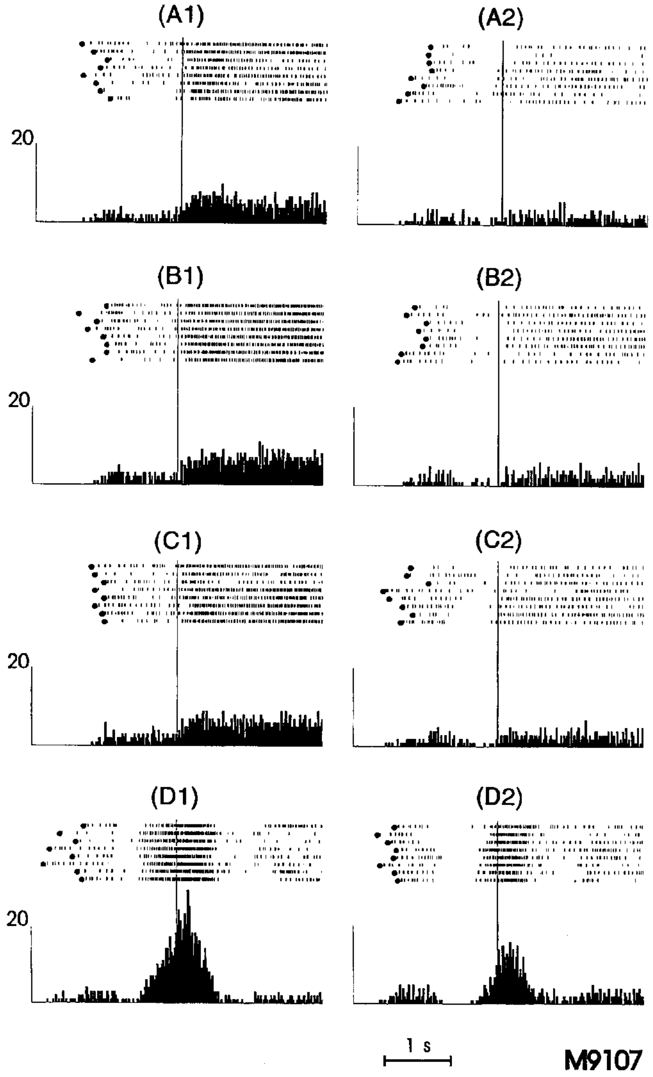

Fig. 6 Hand preference in a holding mirror neuron. A stylus with a piece of food was presented to the monkey, the experimenter made a grasping movement toward the food and then held it with his fingers until the end of the trial. The experimenter's actions were performed using either his left (**A1**, **B1** and **C1**) or right hand (**A2**, **B2** and **C2**). The action was repeated centrally (**A**), on the left (**B**) or on the right (**C**) of the monkey. Note the stronger activation when the left hand was used regardless of where the action was made. **D1** and **D2,** neurons' discharge during monkey's active grasping movement (**D1**, right hand; **D2**, left hand). Note that also during the monkey's active movements the neuron showed hand preference. Conventions as in Fig. 1.

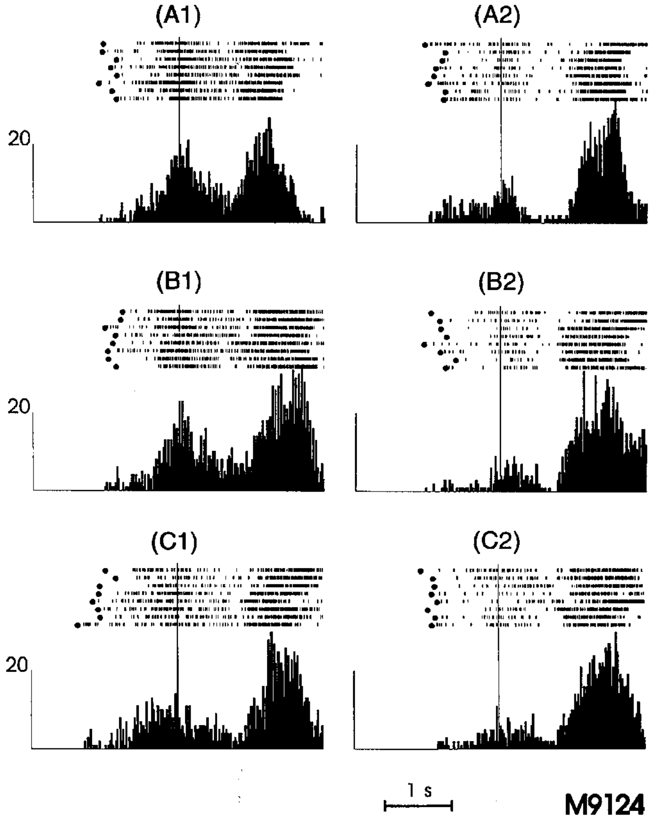

Fig. 7 Action direction preference in a grasping mirror neuron. The experimenter grasped the food, making a reaching movement either from right to left (**A1**, **B1** and **C1**) or from left to right (**A2**, **B2** and **C2**), then moved the food toward the monkey which grasped it. The experimenter's reaching to grasp action was performed centrally (**A**), in the monkey left hemifield (**B**) and in the monkey right hemifield (**C**). Recordings from the left hemisphere. The two discharges present in all panels correspond to the grasping made by the experimenter (observed grasping) and to the monkey's grasping (active grasping). Conventions as in Fig. 1.

Table 3 *Classification of mirror neurons according to their motor properties*

	n	%
Grasping with the hand and the mouth	11	11.9
Grasping with the hand	60	65.2
Grasping with the mouth	9	9.8
Manipulation	8	8.7
Tearing	2	2.2
Bringing to the mouth	2	2.2
Totals	92	100

broad classes: 'strictly congruent', 'broadly congruent' and 'non-congruent'.

We defined those mirror neurons ($n = 29$; 31.5%), in which the effective observed and executed actions corresponded both in terms of general action (e.g. grasping) and in terms of the way in which that action was executed (e.g. precision grip), as 'strictly congruent'. An example of a strictly congruent mirror neuron is shown in Fig. 9. This neuron responded selectively to the observation of the experimenter extracting a small piece of food from a hole with his index finger (Fig. 9A). The same action was the only action made by the monkey that triggered the neuron (Fig. 9B). Note the absence of any discharge when the monkey grasped the food using a precision grip (Fig. 9C).

We defined neurons as 'broadly congruent' ($n = 56$; 60.9%), when there was a link, but not identity, between the

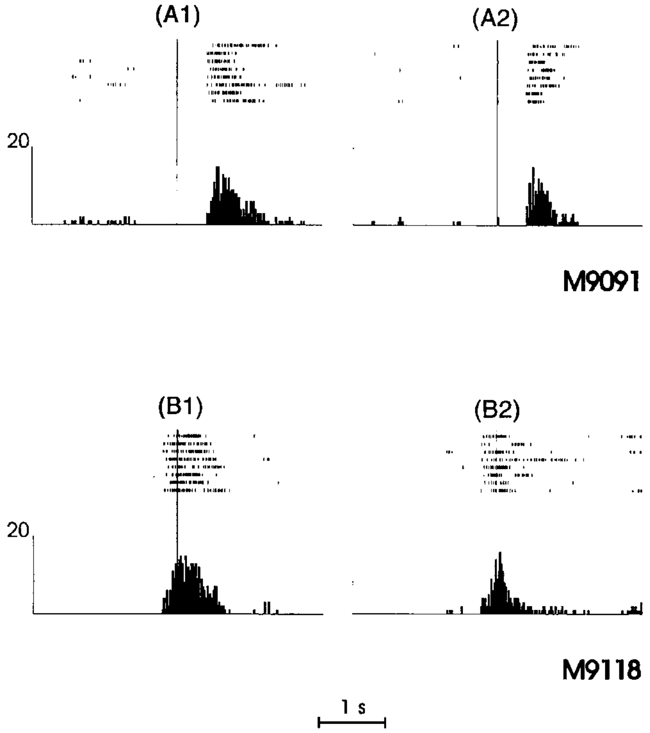

Fig. 8 Motor response of two grasping mirror neurons tested in light (**A1** and **B1**) and darkness (**A2** and **B2**). Neuron M9091 was tested with the apparatus described in Methods. The rasters are aligned with the moment at which the door of the testing box was opened. Neuron M9118 was tested by presenting the monkey with food placed on a tray and allowing it to grasp it. The rasters are aligned with the moment at which the monkey touched the food (lines across trials). Other conventions as in Fig. 1.

effective observed and executed action. Three different groups of broadly congruent neurons were identified.

Neurons of the first group ($n = 7$) were highly specific in terms of motor activity, discharging in association not only with a single type of hand action (grasping or holding), but also with a specific type of grip (e.g. precision grip, finger prehension, whole hand prehension). However, unlike the similar strictly congruent neurons, they responded to the observation of various types of grips (e.g. precision grip and whole hand prehension). Figure 10 shows a typical neuron belonging to this group. This neuron became active when the monkey observed the experimenter grasping an object with a precision grip (Fig. 10A) or with a whole hand prehension (Fig. 10B). The motor response was present when the monkey grasped food with a precision grip (Fig. 10C), but not with a whole hand prehension (Fig. 10D).

A second group of broadly congruent mirror neurons was constituted of neurons ($n = 46$) that became active during one motor action made by the monkey (e.g. grasping, holding or manipulating), but visually responded to two or more different hand actions (e.g. manipulation and grasping).

The last group of broadly congruent neurons ($n = 3$) appeared to be activated by the goal of the observed action regardless of how it was achieved. All these neurons discharged only during active monkey's hand grasping

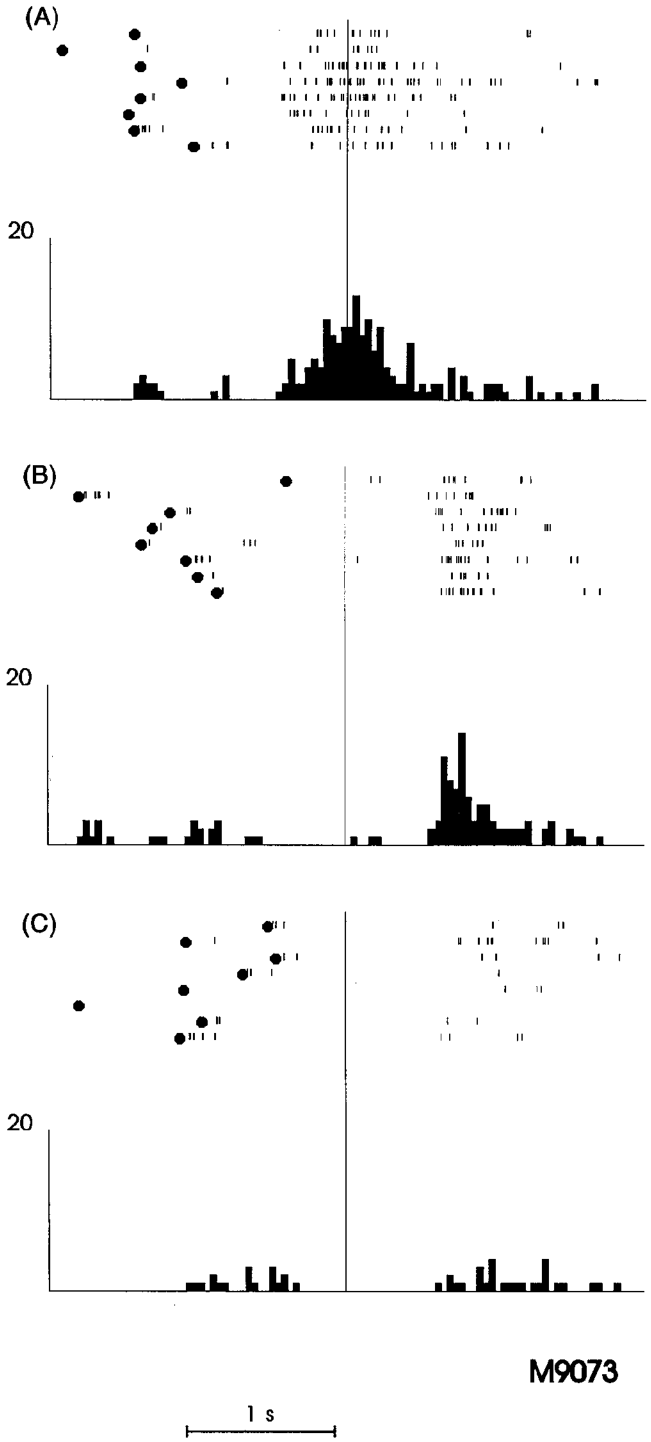

Fig. 9 Example of a strictly congruent manipulating mirror neuron: (**A**) the experimenter retrieved food from a well in a tray; (**B**) same action, but performed by the monkey; (**C**) the monkey grasped a small piece of food using a precision grip. In **A** the rasters are aligned with the moment at which the experimenter touched the food (line across trials). In **B** and **C** the movements were studied using the testing box. The rasters are aligned with the moment at which the door of the testing box was opened. Histograms bin width = 40 ms. Other conventions as in Fig. 1.

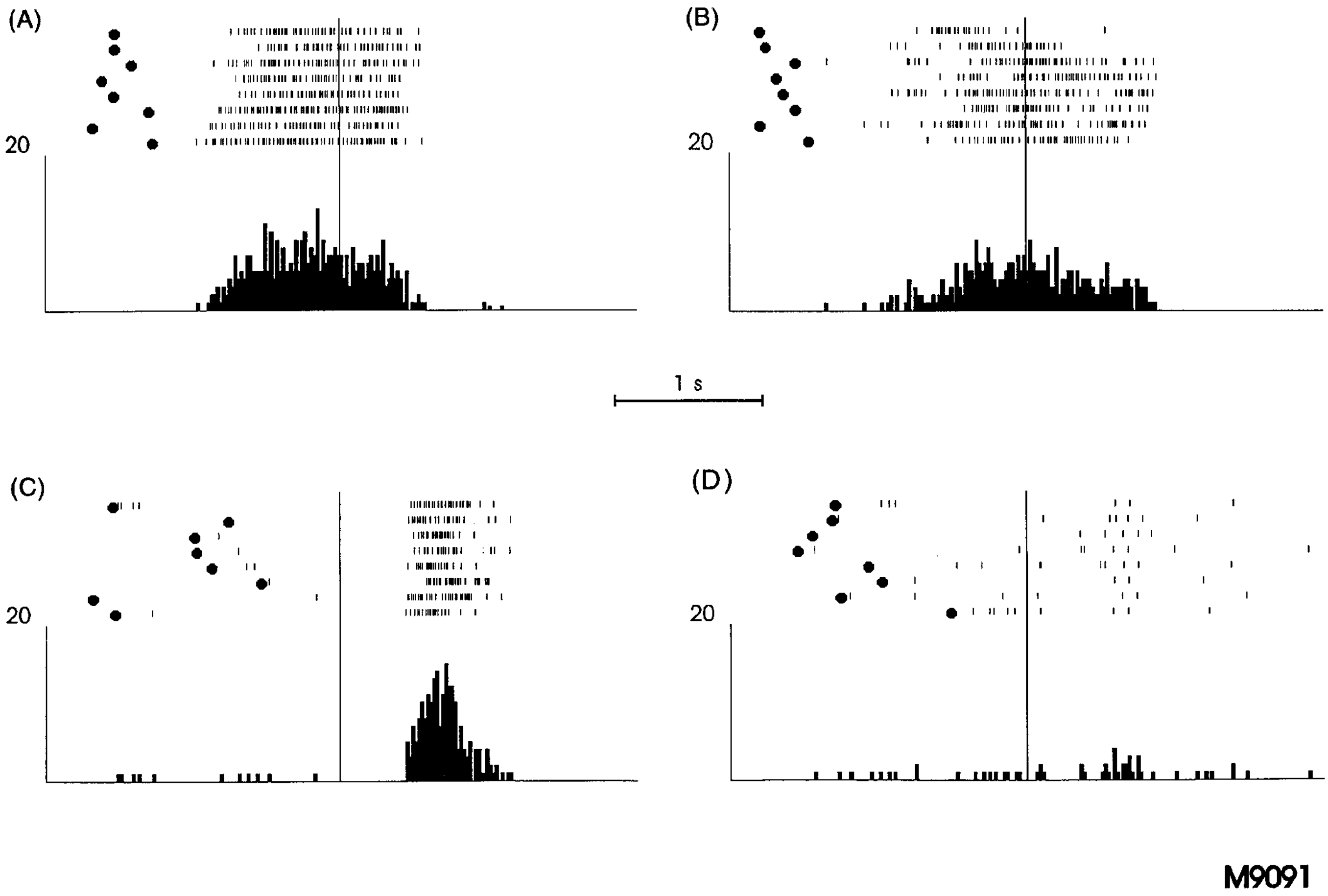

Fig. 10 Example of a broadly congruent grasping mirror neuron: (**A**) the experimenter grasped a piece of food with a precision grip; (**B**) the experimenter grasped an object with a whole hand prehension; (**C**) the monkey grasped a piece of food with a precision grip; (**D**) the monkey grasped an object with a whole hand prehension. In **A** and **B** the rasters are aligned with the moment at which the experimenter touched the food (line across trials). In **C** and **D** they are aligned with the moment at which the door of the testing box was opened. In the case of active movements, the neuron showed a strong specificity for precision grip. Conventions as in Fig. 1.

movements, while, passively, they were activated by the observation of mouth or hand grasping movements made by the experimenter.

Finally, we defined those neurons ($n = 7$; 7.6%) in which there was no clear-cut relationship between the effective observed action and the effective movement of the monkey as 'non-congruent'.

Control experiments

EMG recordings

Typically, food presentation, its placing on a plane and its grasping made by the experimenter did not evoke any overt hand or mouth monkey's movement. However, this fact did not exclude the possibility that the experimenter's action could induce some activity in the hand or face muscles involved in the execution of the observed action which might have passed unnoticed to pure observation.

To control for this possibility, we recorded the EMG activity from several hand and mouth muscles in experimental sessions specifically devoted to this purpose. Figure 11 illustrates one of these experiments. The activity of four hand and mouth muscles is shown during testing of mirror properties and during food movement towards the monkey and its grasping of it. Note that no EMG activity was present during all these phases except during monkey's active movements.

Activity of F1 (area 4) neurons during action observation

A further control that no motor activity related to the observed action was present during action observation was made by recording single neurons from the hand field of F1. The rationale of the experiment was that if movements observed by the monkey would trigger analogous monkey's movements, neurons in the primary motor cortex (F1) that control them should fire as mirror neurons do in F5. The results showed that none of the recorded neurons ($n = 49$) discharged during the observation of actions performed by the experimenter.

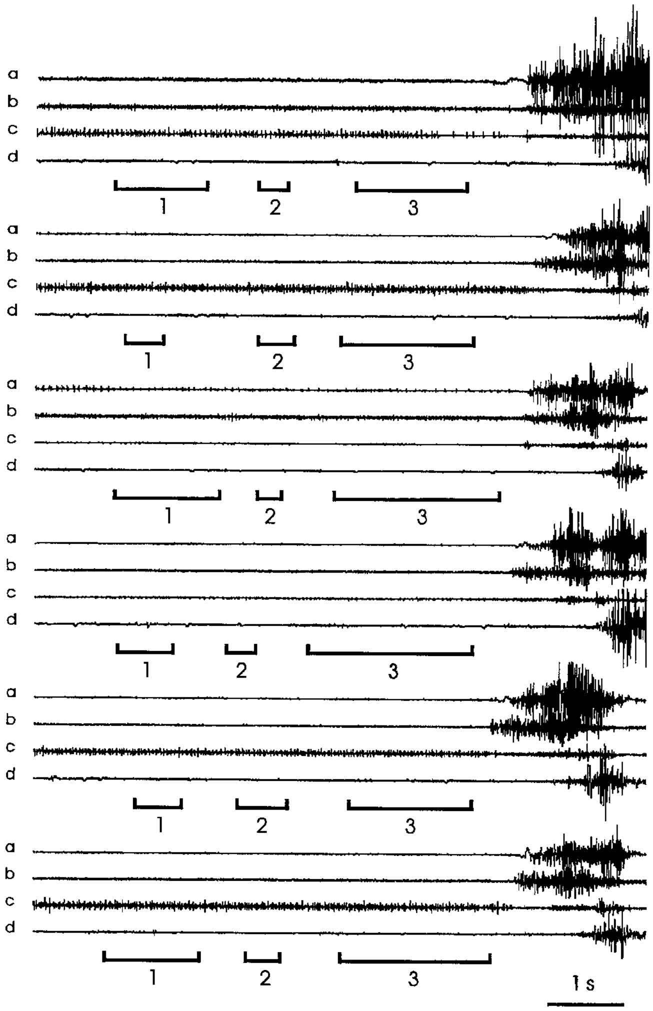

Fig. 11 Muscle activity during standard testing of mirror neurons. The EMG was recorded from three hand muscles (a, opponens pollicis; b, flexor digitorum superficialis; c, extensor digitorum communis) and from the orbicularis oris (d). Six successive trials of 8 s are presented. The sequence of the events was the following: the experimenter showed a piece of food to the monkey (1), placed it on a tray (2), grasped and manipulated it (3), gave it to the monkey. The monkey's active grasping was accompanied by an intense EMG activity. Note the absence of any EMG changes during the other events.

Location of the recorded neurons

The location of the recorded neurons was histologically assessed in the two hemispheres of one monkey (MK8). Figure 12 shows a lateral view of the two hemispheres and an enlarged view of the agranular frontal cortex between the central and arcuate sulci. Filled circles indicate the penetrations from which mirror neurons were recorded. The size of the circles is proportional to the number of mirror neurons found in that penetration. Note the absence of mirror neurons in the penetrations made in F1.

Microstimulation of F5, histologically determined in MK8, elicited movements of the wrist and fingers, while the microstimulation of the adjacent F4 evoked neck and proximal arm movements. A similar caudo-rostral pattern of proximal–distal movement representation was found also in MK9 and used to locate F5 functionally in this monkey. The motor properties of the recorded neurons confirmed this location.

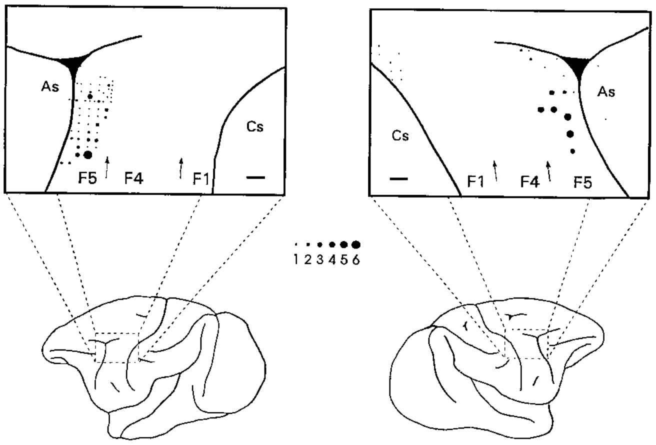

Fig. 12 Location of microelectrode penetrations in one monkey (MK8). The lateral views of the two hemispheres are shown below the enlarged views of the explored cortex. The penetrations performed in areas F5 and F1 are indicated by dots. Dot size is calibrated according to the number of mirror and mirror-like neurons found in a given penetration. Arrows indicate the borders between the cortical areas. As = arcuate sulcus; Cs = central sulcus. Calibration bars = 1 mm.

Discussion

Previous studies showed that area F5 is an area functionally related to goal-directed hand movements. Most neurons in this area are selectively activated during particular types of prehensions. Some discharge also at the presentation of three-dimensional visual objects (Rizzolatti *et al.*, 1988).

The present findings indicate that there are other neurons in F5 (mirror neurons) that, although undistinguishable from those presented before, as far as their motor properties are concerned, respond selectively to the sight of actions made by other individuals. It appears, therefore, that different classes of F5 neurons can be activated either by object presentation or by the sight of a motor action. In the next paragraphs we will discuss the properties of this new class of F5 neurons. We will conclude by speculating on the generality of the present findings and on their importance for the understanding of the mechanisms at the basis of action comprehension.

Visual properties

Agent of action

The visual responses of mirror and mirror-like neurons resulted from an interaction of the agent of the action with the object target of the action. The sight of the agent alone or of the object alone was ineffective. Even when the monkey saw both the hand miming an effective action and an object appropriate for it, the response was absent when the action was not directed toward the object.

Hand and mouth actions were by far the most effective agents. The responses to tools or to objects moved in such a way as to imitate the effective action were usually weak or absent altogether. There was a large amount of generalization as far as the precise physical aspects of the effective agent were concerned. For many neurons there was no difference between right and left hand and the precise hand orientation was not crucial in activating the neuron. Similarly, the distance between the executed action and the monkey in most cases did not influence the response.

A few neurons were equally activated by hand and mouth movements provided they had the same goal. In this case the equivalence was, obviously, not based on visual similarities but on the meaning of the action. Consistent with this finding is the presence in F5 of neurons that discharge during hand and mouth active movements having the same behavioural meaning (Gentilucci and Rizzolatti, 1990). The number of mirror neurons showing perceptual mouth–hand generalization was, however, rather small in the present sample. It is possible that this was a consequence of the location of our penetrations, located essentially in the F5 hand field.

Some neurons appeared to respond selectively to the direction of hand movements. Typically, they preferred the movements directed towards the recorded side. There are two possible explanations for this finding. The first is that these neurons were indeed directionally selective neurons. The second is that they coded a specific hand–arm orientation. When a hand movement is made in front of an observer there is an invariant relationship between the position of the hand and that of the arm, irrespective of the hand used. When hand movements are made from right to left (with respect to the observer), the arm is always on the right of the hand and, conversely, when hand movements are made from left to right the arm is always on the left of the hand. It is possible, therefore, that the mirror neurons that appeared to be selective for a movement direction were, in fact, selective for a particular arm–hand moving configuration.

Object of action

Mirror and mirror-like neurons were unselective for the object significance. The responses to meaningful objects like food were the same as those to three-dimensional solids, the only difference being the constancy of the responses. It is likely that this was due to the fact that the monkey tended not to pay attention to uninteresting objects after a few or even the first presentation.

As for the size of the object acted upon, most neurons were not influenced by this factor. Exceptions to this were some mirror grasping and manipulating neurons that discharged much stronger when the objects grasped or manipulated by the experimenter were of a particular size. The selectivity was related to the real size of the object and not on its size on the retina. The same neurons fired vigorously when an action was made upon a small object near the monkey or far (1 m) from it, whereas they did not fire when the same action was made on a large object close to or far from the monkey. Since, however, we have not tested mirror and mirror-like neurons with ambiguous objects that could be grasped with different grips, we do not know whether the selectivity of these neurons were due to the size of the presented objects or to the grip that their size evoked.

Neurons responding to complex stimuli located in other cortical regions

Areas directly connected to F5

F5 has no direct input from visual occipital areas. Its main cortical input comes from inferior parietal lobe and, in particular, from (Matelli *et al.*, 1994) and from the anterior intraparietal area (AIP) area 7b (Godschalk *et al.*, 1984; Petrides and Pandya, 1984; Matelli *et al.*, 1986; Cavada and Goldman-Rakic, 1989; Andersen *et al.*, 1990). Area AIP was extensively studied by Sakata and his co-workers (Taira *et al.*, 1990; Sakata *et al.*, 1992*a, b*; Sakata and Taira, 1994). Their data showed that the organization of this area shares many commons aspects with F5. No neuron, however, was found that responds to the sight of the experimenter's hand interacting with an object (*see* Jeannerod *et al.*, 1995).

The most detailed studies of area 7b are still those performed by Hyvärinen and his co-workers many years ago (Leinonen and Nyman, 1979; Leinonen *et al.*, 1979; Hyvärinen, 1981). They found that many neurons in area 7b responded to somatosensory, visual and both somatosensory and visual stimulation. Some neurons were activated by 'intentional' movements and especially by reaching and manipulation. Among neurons responding to visual stimulation they reported one neuron that 'fired when the experimenter's hand approached a package of raisins' (*see* Leinonen *et al.*, 1979, p. 306). They did not comment on the surprising properties of this neuron, possibly because of its rarity. Given our present findings, however, it is possible that that neuron is less exceptional than it appeared. Possibly neurons with mirror or mirror-like properties are present in 7b, but have not been detected for lack of systematic (and appropriate) testing.

Superior temporal sulcus region

Neurons with visual properties similar to those of mirror neurons are rather numerous in the region of the superior temporal sulcus and, particularly, in its lower bank (area TEa of Seltzer and Pandya, 1989) (Perrett *et al.*, 1982, 1989, 1990). The similarities between the properties of F5 and superior temporal sulcus neurons are striking. Both populations of neurons appear to code the same actions, generalize their responses to different instances of the same action, do not respond to hand movements miming the preferred action in the absence of the object, and do not respond to object–object interaction, even when the moved object is similar to an arm and hand. Neurons that prefer a certain direction of actions were not reported in superior temporal sulcus. It is possible that these neurons are present only in F5. The major difference, however, between F5 and superior temporal sulcus neurons, is that only in F5 are there neurons that both respond to complex visual stimuli and have movement-related activity.

The presence of two brain regions with neurons remarkably similar in their responses to visual stimuli, raises the question of their possible relationships. One possibility is that the two representations of hand–object interactions are independent one of another and have different functional roles. In view of the distinction between pragmatic and semantic cortical maps (Goodale and Milner, 1992; Jeannerod, 1994; Milner and Goodale, 1995), one can postulate that superior temporal sulcus is the semantic representation of hand–object interactions, while F5 is the pragmatic one. Another possibility is that the two representations are stages of the same analysis. The superior temporal sulcus representation would provide, in this case, an initial description of hand–object interactions that would then be sent to F5 and matched with the 'motor vocabulary' (Gentilucci and Rizzolatti, 1990; Jeannerod *et al.*, 1995) of that area. The two possibilities are not mutually exclusive. The superior temporal sulcus representation might be both a semantic representation and a stage for further matching with motor actions.

Possible functional role of mirror neurons

In monkey's area 6, there are neurons ('set-related' neurons) that discharge before the movement onset, when the target of the impending movement is pre-specified (Weinrich and Wise, 1982; Wise and Mauritz, 1985; Kurata and Wise, 1988*a*, *b*; Alexander and Crutcher, 1990; Rizzolatti *et al.*, 1990; Mushiake *et al.*, 1991). An explanation of mirror neurons in terms of motor preparation appears to be, at least at first glance, plausible. It is possible that when the monkey observes a certain action made by another individual, it starts to prepare that action in order to execute it as fast as possible.

There are two main arguments against this interpretation of mirror neuron function. The first is that the monkey that observes an action does not emit it during its observation or immediately after. Secondly, mirror neurons stop firing when the object grasped or manipulated by the experimenter is moved toward the monkey and becomes more available to it. They start to discharge again only when the monkey makes the movement. If the firing of mirror neurons were related to motor preparation of the observed action, their activity should continue through the period between observation and movement (*see* Fig. 1).

An alternative interpretation of the mirror neurons function is that their discharge generates an internal representation of the movement (*see* Jeannerod, 1994). This representation may have different complementary functions, among which motor learning and the understanding of meaning of the observed action.

It is well known that both adults and children learn by imitation. This imitation process could be based on an observation/execution matching mechanism similar to that represented by mirror neurons. Such a mechanism can, on the one hand, extract the essential elements describing the agent of the action (hand, arm, face) and, on the other, code them directly on specific sets of neurons with motor properties like those of F5 'motor vocabulary'.

Another possible function of mirror neuron movement representation is that this representation is involved in the 'understanding' of motor events (di Pellegrino *et al.*, 1992). By this term we mean the capacity to recognize that an individual is performing an action, to differentiate this action from others analogous to it, and to use this information in order to act appropriately. Self-consciousness is not necessarily implied in these functions (Rizzolatti, 1994).

When an individual emits an action, he 'knows' (predicts) its consequences. This knowledge is most likely the result of an association between the representation of the motor act, coded in the motor centres, and the consequences of the action. Mirror neurons could be the means by which this type of knowledge can be extended to actions performed by others. When the observation of an action performed by another individual evokes a neural activity that corresponds to that which, when internally generated, represents a certain action, the meaning of it should be recognized, because of the similarity between the two representations.

Mirror system in humans

The mirror system provides a way to match observation and execution of events. Does such a system exist in humans? There are two sets of evidence that strongly suggest that this is indeed the case.

The first is based on transcranial magnetic stimulation of the motor cortex in normal human subjects (Fadiga *et al.*, 1995). In these experiments, subjects were stimulated during observation of an experimenter grasping three-dimensional objects, during observation of the same objects, and during the detection of the dimming of a small spot of light. The results showed a significant increase of motor evoked potentials recorded from the hand–arm muscles during grasping observation with respect to the other conditions. The increase was present only in those muscles that were recruited when the subjects made the observed movements actively.

The finding of an increase in cortical motor excitability during grasping observation may appear, at least a first glance, in contrast with the present finding that F1 (area 4) neurons do not discharge during action observation. The increase of motor evoked potentials, however, does not necessarily imply an activation above threshold of primary motor cortex neurons. Such an increase could have resulted from a subthreshold activation of primary motor cortex, from an activation of premotor areas that influence, directly or via brainstem, the excitability of the spinal chord, or from both these activations.

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The second evidence derives from a PET study (Rizzolatti *et al.*, 1996*b*) in which regional cerebral blood flow was measured during object observation, grasping observation and object prehension. The most important result was that during grasping observation there was an activation of the region of the superior temporal sulcus and of the posterior part of the inferior frontal gyrus (Broca's area) (*see* Rizzolatti *et al.*, 1996*a*).

These data are in good agreement with the monkey single neuron data discussed above showing that F5 and the region within the superior temporal sulcus are the two cortical regions where neurons responsive to motion of body parts are located. A point, however, that deserves some comment is the activation of human inferior frontal gyrus.

It is generally agreed that the caudal part of this gyrus is the cortical homologue of monkey F5 (Petrides and Pandya, 1994; also *see* Passingham, 1993). However, while F5 contains both a mouth and a hand representation, the caudal part of the inferior frontal gyrus is classically considered as a speech area (Broca's area). It should therefore contain a representation of effectors related to language production, but not to hand movements. Is this really true? Is the Broca's area indeed exclusively a speech area?

There are several arguments indicating that is not so. A first argument is an evolutionary one. A distal movement representation rostral to that of area 4 (F1) and located in the antero-ventral part of the agranular frontal cortex is common to all studied primates (Nudo and Masterton, 1990). Considering the great development (and sophistication) of human manual dexterity, it is very hard to imagine that what appears to be the most important premotor area for hand and finger movements would have disappeared precisely in man.

A second argument derives from two recent PET studies. Bonda *et al.* (1994) found that during the execution of a self-ordered hand movement sequence, there was a highly significant increase of blood flow in correspondence with Broca's area. Parsons *et al.* (1995) describe an experiment in which they asked subjects to recognize if the pictures of a hand represented the left or the right hand, and found a strong activation of area 44 extending rostrally into area 45. This task, in order to be executed, required subjects to form a mental imagery of their hand and subsequently to rotate it.

A third argument comes from clinical observations. It is well established that aphasic patients, including those with frontal lesions, are frequently impaired in pantomime recognition (Brain, 1961; Gainotti and Lemmo, 1976; Duffy and Watkins, 1984; Bell, 1994). Although it was suggested that the pantomime recognition deficit could depend on a concomitant lesion of cortical areas adjacent to Broca's area (Goodglass and Kaplan, 1963), the evidence reviewed above supports the opposite view, i.e. that responsible for the deficit is a lesion of the Broca's area and, more precisely, that part of it where hand actions are represented. What is particularly interesting for the present discussion is that the pantomime deficit following Broca's lesion is exactly the kind of deficit that one would predict if the Broca's area had a mechanism for action recognition like that described in the present paper. Taken together, the different lines of evidence reviewed above appear to indicate that both F5 and Broca's area have a hand movement representation and that, probably, they are both endowed with a similar mechanism for action recognition.

A final point worth noting is that the mechanism matching action observation and execution discussed in the present article is very similar to that proposed by Liberman and his colleagues for speech perception (motor theory of speech perception) (Liberman *et al.*, 1967; Liberman and Studdert-Kennedy, 1978; Liberman and Mattingly, 1985). According to this theory, the objects of speech perception are not to be found in the sounds, but in the phonetic gesture of the speaker, represented in the brain as invariant motor commands. The phonetic gestures are 'the primitives that the mechanisms of speech production translate into actual articulatory movements, and they are also the primitives that the specialized mechanisms of speech perception recover from the signal' (Liberman and Mattingly, 1989). Although our data concern essentially hand actions, however, considering the homology between monkey F5 and human Broca's area, one is tempted to speculate that neurons with properties similar to that of monkey 'mirror neurons', but coding phonetic gestures, should exist in human Broca's area and should represent the neurophysiological substrate for speech perception.

Acknowledgements

We wish to thank A. H. Fagg for discussion of the data and L. Luppino, M. Matelli and A. Palmeri for their help in part of the experiments. The work was supported by the Human Frontier Science Program and by grants from CNR and MURST to G.R.

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Received October 3, 1995. Accepted October 31, 1995