

Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex

Pier Francesco Ferrari,¹ Vittorio Gallese,¹ Giacomo Rizzolatti¹ and Leonardo Fogassi^{1,2}

¹Dipartimento di Neuroscienze, Università di Parma, via Volturno 39, 43100 Parma, Italy

²Dipartimento di Psicologia, Università di Parma, B.go Carissimi 10, 43100 Parma, Italy

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Abstract

In the ventral premotor cortex (area F5) of the monkey there are neurons that discharge both when the monkey performs specific motor actions and when it observes another individual performing a similar action (mirror neurons). Previous studies on mirror neurons concerned hand actions. Here, we describe the mirror responses of F5 neurons that motorically code mouth actions. The results showed that about one-third of mouth motor neurons also discharge when the monkey observes another individual performing mouth actions. The majority of these ‘mouth mirror neurons’ become active during the execution and observation of mouth actions related to ingestive functions such as grasping, sucking or breaking food. Another population of mouth mirror neurons also discharges during the execution of ingestive actions, but the most effective visual stimuli in triggering them are communicative mouth gestures (e.g. lip smacking). Some also fire when the monkey makes communicative gestures. These findings extend the notion of mirror system from hand to mouth action and suggest that area F5, the area considered to be the homologue of human Broca’s area, is also involved in communicative functions.

Introduction

Area F5 forms the rostral part of the monkey ventral premotor cortex. Electrical microstimulation and single neuron recording studies showed that area F5 is involved in the control of hand and mouth movements (Rizzolatti *et al.*, 1981; Kurata & Tanji, 1986; Rizzolatti *et al.*, 1988; Hepp-Reymond *et al.*, 1994). The representation of hand movements occupies essentially the dorsal part of F5, whereas that related to mouth movements is mostly located in its ventral part (Gentilucci *et al.*, 1988).

A fundamental functional property of area F5 is that many of its neurons do not discharge in association with elementary movements, but become active during goal-directed actions such as grasping, tearing or manipulating objects (Rizzolatti *et al.*, 1988). Some of them also discharge in response to visual stimuli. These neurons (visuo-motor neurons) have been subdivided into two classes: ‘canonical’ neurons and ‘mirror’ neurons (Rizzolatti *et al.*, 2000).

Canonical neurons are neurons that become active when the monkey observes, remaining still, three-dimensional visual stimuli whose size and shape is congruent with the type of hand shape coded by the neuron (Rizzolatti *et al.*, 1988; Murata *et al.*, 1997). These neurons are considered to be involved in visuo-motor transformations necessary for object-directed actions (Jeannerod *et al.*, 1995).

Mirror neurons are those neurons that become active both when the monkey performs a motor action and when it observes a similar action made by another individual. The presentation of three-dimensional objects is ineffective in triggering mirror neurons, even when stimuli of particular interest for the monkey, such as food, are pre-

sented (Di Pellegrino *et al.*, 1992; Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996).

An important property of mirror neurons is the congruence they show between the effective observed and the effective executed action. This congruence may be very strict such that only the observation of an action virtually identical to that motorically coded by a given neuron may activate it. Most frequently, however, the congruence is in terms of the goals of the observed and executed action, rather than in terms of movements necessary to achieve it. On the basis of these properties, it was suggested that F5 mirror neurons are part of a neural system matching the visual description of an action with its execution and that this observation/execution matching system plays a role in action understanding (Rizzolatti *et al.*, 2001).

The study of mirror neuron properties was limited up to now to neurons that discharge in association with hand actions (Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996). The aim of the present study was to assess whether there is also a mouth mirror neuron system in F5. The demonstration of its existence would be of great interest given the importance of oro-facial actions recognition during social interactions.

Materials and methods

General procedures

All macaque monkeys (*Macaca nemestrina*) used in this study came from a colony of the Centre de Primatologie, Université Louis Pasteur, Strasbourg, France. The experiments were carried out on two awake (monkey 1 and monkey 2), partially restrained macaque monkeys. All experimental protocols were approved by the Veterinarian Animal Care and Use Committee of the University of Parma as well as by the Italian Ministry of Health. All experiments complied with the European law on the humane care and use of laboratory animals.

Correspondence: L. Fogassi, as above.
E-mail: fogassi@unipr.it

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Before starting the experiments, the monkeys were habituated to the experimenters and the experimental conditions. The monkey was seated in a primate chair and trained to observe the experimenter making various hand and mouth actions such as taking the food from a container, manipulating it and eventually either giving it to the monkey or moving it toward its own mouth. This pretraining was important for subsequent testing of the neuron's motor properties (see below) and for habituating the monkey to pay attention to the experimenters and their actions.

The surgical procedures for neuron recordings were the same as previously described (Fogassi *et al.*, 1996) with each animal anaesthetized with ketamine hydrochloride (15 mg/kg *i.m.*). The head implant included a head holder and a chamber for single-unit recordings. Neurons were recorded using tungsten microelectrodes (impedance 0.5–1.5 M Ω , measured at 1 kHz) inserted through the dura that was left intact. Neuronal activity was amplified and monitored on an oscilloscope. Individual action potentials were isolated with a dual voltage-time window discriminator (Bak Electronics, Germantown MD, USA). The output signal from the voltage-time discriminator was monitored and fed to a PC for analysis.

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

Recording sites

The chamber for single-unit recordings was implanted stereotactically. The chamber rostro-caudal and medio-lateral axis dimension (20 mm \times 15 mm) was such as to allow to record from the whole ventral premotor cortex, from area F1 (primary motor cortex) to the caudal part of the frontal eye fields (FEF) included. After chamber implantation the ventral part of the agranular frontal cortex was functionally explored (single neuron recordings and intracortical microstimulation) in order to assess the location of areas F1 (primary motor cortex), F4 and F5 (ventral premotor cortex) and to find out the sector of F5 where neurons related to mouth actions are mostly located. For the criteria used to functionally characterise areas F1, F4 and F5, see Umiltà *et al.* (2001). Once the mouth sector of F5 was identified, penetrations were concentrated in this sector and neurons whose activity was associated with mouth movements studied.

Neuron testing

Each neuron, once isolated, was tested in order to ascertain its motor and visual properties.

Motor properties

Neurons discharging in association with active hand actions were tested using the same stimuli and procedures as in previous studies. Briefly, the monkey was presented with a variety of objects of different size and shape. They consisted of food items and objects at hand in the laboratory. The objects were presented in different part of space within and outside the reaching distance of the monkey. The monkey was trained to fixate them and, when at reaching distance, to grasp them (for details, see Rizzolatti *et al.*, 1988; Rizzolatti *et al.*, 1990).

Neurons discharging in association with mouth actions were studied by eliciting a variety of mouth actions. The following procedures were used. (i) Presentation of food that could be eaten without the necessity to break it. The following food was presented: pieces of apples of different size, raisins and peanut seeds. The food was moved towards the mouth and the monkey took it with its teeth (grasping) or with its lips (grasping with lips). Alternatively the food was moved toward the

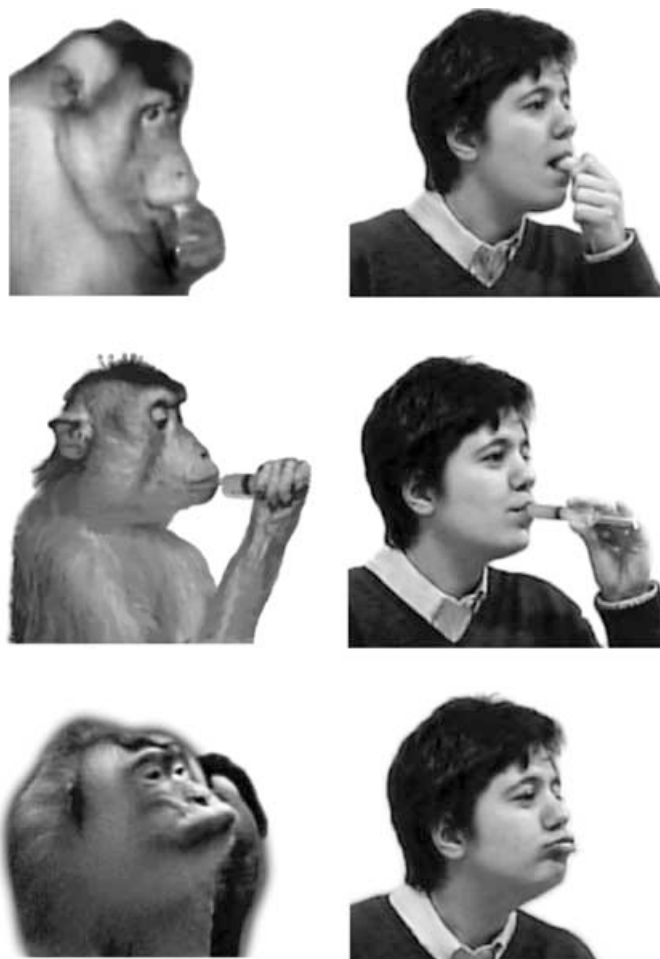


FIG. 1. Examples of transitive and intransitive actions performed by the experimenter in front of the recorded monkey (right column); same gestures made by the monkey (left column). Intransitive monkey actions, although rarely evoked during recording sessions, are shown here to outline their similarity with the same actions performed by the experimenter. From top to bottom: grasping of a piece of food; sucking juice from a syringe; lips protruded face.

monkey who grasped it with its hand and then introduced it into the mouth. Subsequently the monkey chewed the food (chewing) and ate it. (ii) Presentation of food that required breaking (breaking). In this case food consisted of crackers or of sunflower seeds. In the latter case the monkey broke the seed shell with its teeth and ate the content. (iii) Administration of water or fruit juice with a syringe (sucking). (iv) Letting drops of fruit juice fall from a syringe close to the mouth. The monkey protruded its tongue to get it. Protrusion was followed by retraction (reaching with the tongue). (v) Giving the monkey pieces of solid food without allowing the monkey to take it into the mouth. The monkey bit the food holding it with incisor teeth (holding with the mouth). Figure 1 (left side) shows two of these actions. Figure 1 shows also a communicative gesture (lowest panel, lips protrusion) made by the monkey. (For the description of communicative gestures and the way in which we elicited them, see below).

Visual properties

Once established the neuron's motor properties, its visual properties were tested by performing hand and mouth actions in front of the monkey.

In a preliminary phase of this study video-recorded actions were presented to the monkeys. These actions were recorded using

a three-dimensional (3-D) system. This system is constituted of two video-cameras (xc-999p, SONY), a 3-D to 2-D switching box (vrmux2p, VREX), a card and a 3-D projector (VR2100, VREX). Several different hand and mouth actions performed by the experimenter or by the monkey were recorded. Most of the video material about macaque gestures recorded with a 3-D system was provided by the Kyoto Primate Centre. Video clips were then stored in a computer. During the experiments, the video clips were presented to the monkey on a screen (180 × 160 cm) by means of the 3-D projector. A switch allowed us to present both 2-D and 3-D video clips of the same action. We focused on mirror neurons responding to the observation of hand actions because their properties are well defined. The results were very disappointing. Mirror neurons that, during naturalistic testing, showed good responses to a hand action made by the experimenter, showed weak or no response when the same action, previously recorded, was shown on the screen. A similar observation was reported by Hari and coworkers in human subjects (Jarvelainen *et al.*, 2001). These authors found that brain activation as recorded by MEG was higher when subjects observed hand actions made in a natural situation than when they observed hand actions presented on a screen. Given these interesting but disappointing (at least for the purpose of the present experiment) results, the procedure of presenting video-recorded material was not further used. Thus, all neurons whose properties are described in the present study have been tested by hand and mouth actions made by the experimenters in front of the monkey.

Visual responses to the presentation of hand actions were studied as in our previous experiments on hand mirror neurons (Gallese *et al.*, 1996). The tested actions were: object grasping, holding, manipulating, breaking and tearing. In order to assess whether the recorded neuron coded specifically hand-object interactions, the following stimuli were also presented to the monkey: movements of the hand miming grasping in the absence of the object and grasping of food or other objects with tools (e.g. forceps, pincers).

Visual responses to mouth actions were studied by performing a series of mouth actions in front of the monkey. These actions were: grasping, holding, breaking (in these three gestures the food could be either placed on a surface, or held by a stick or by the experimenter's hand), sucking, reaching with the tongue (the syringe was held by a tool or directly by the experimenter's hand), taking away (the experimenter approached with the head a piece of food placed on a surface or a stick, grasped it with the mouth and took it away from its support) and chewing. Two of the presented actions are shown in Fig. 1 (right side, upper and middle panels).

In addition to ingestive actions, all neurons were tested with a second series of actions belonging to the macaque communicative behavioural repertoire (see van Hooff, 1967; Maestriperi, 1996). These actions were lip smacking, lips protrusion (Fig. 1, right lower panel), teeth-chatter and open-mouth face. Fragments of these communicative gestures, such as tongue protrusion or eyebrows lifting, were also presented.

The presentation of communicative gestures made by the experimenter only rarely elicited a communicative motor response during neuron recording. This is probably related to the fact that the communicative gestures were made by the experimenter, that is, by a noncon-specific. However, as the monkeys did not react to the film presentation of monkey's communicative gesture, communicative gestures made by an experimenter was the only way to elicit a communicative response. On the other hand, the fact that the monkeys recognised the communicative gestures made by the experimenters was proved by a behavioural experiment described below (see Results).

All the above described mouth/face actions were performed by an experimenter standing in front of the monkey. The experimenter's

gesture could be performed either facing the monkey or directing the head to the right or to the left. The actions were presented to the monkeys mostly by two experimenters (PF and LF) and, occasionally, also by the others. Although the two monkeys were particularly familiar with the experimenter (PF) who trained the monkey before recording, no obvious difference in neuron response related to which experimenter performed the action was observed (see also below).

Eye movements and EMG recordings

Eye movements were studied in two monkeys (monkey 3 and monkey 4) submitted to the same training procedure and experimental conditions as the monkeys used for neuronal recording. Four ingestive and four communicative mouth actions were presented. The ingestive actions were grasping, breaking, sucking and reaching with the tongue; the communicative gestures were: lip-smacking, lips protrusion, tongue protrusion and open mouth. All actions were presented by an experimenter to the monkeys seated on the primate chair, with the head fixed, in the same recording room and in the same environmental context. Each action was presented in blocks of 10 trials. A video camera was positioned behind the experimenter. In this way it was possible to record at the same time the monkeys eyes and the experimenter's mouth actions reflected on a mirror located behind the monkeys head. Two experimenters (one of them naive to the objectives of the experiment) analysed the videotapes reporting the monkeys' eye position during each experimenter's action. A slow-motion system enabled us to analyse single frames. Each second of recording contained 25 frames.

EMG was recorded bipolarly from the orbicularis oris and masseter muscles using Ag-AgCl surface electrodes (diameter 15 mm) fixed on the skin by means of gluey material. The EMG recordings were made in specific sessions devoted to EMG control. The testing procedures were the same as those used during neuron recording. Recordings were made simultaneously from monkey's and experimenter's muscles while the experimenter performed the following ingestive and communicative actions: grasping, sucking, lip smacking and lips protrusion. In addition, an EMG was recorded from the monkey's muscles while the monkey performed the two ingestive actions mentioned above. EMG signal was amplified (gain × 10), band pass filtered (10–1000 KHz) using a Dantec electromyograph (Dantec, Skovlunde, Denmark). The signal was then converted with a Digital Analog Card and stored on a PC for successive analysis.

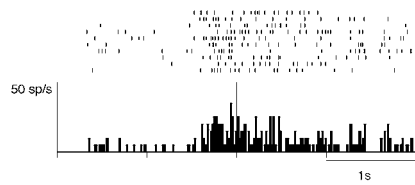
Data analysis

After neuron visual and motor characterisation, 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 hand or their mouth. This signal was used to align the trials and, subsequently, to construct the response histograms. In the case of communicative actions and, more generally, in the case of intransitive (non-object directed) actions, the experimenter pressed a switch when the dynamic phase of the action was concluded (e.g. during lips protrusion when the lips were fully protruded and kept in protruded position). In the case of lip smacking and other repetitive actions, the switch was pushed at the action onset. Switch pushing produced a signal that was used for the response alignment. Response histograms were constructed by summing 10 individual trials. Unless some technical problems did not interfere with trial acquisition (e.g. delays in closing the contact detecting circuit) no trials were discarded.

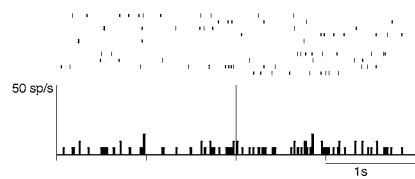
In order to assess statistically the neuron discharge, the neuronal activity, expressed as mean firing rate (spikes/s), was measured in the

Neuron 68

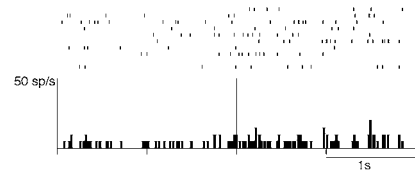
A) Experimenter grasps food with the mouth



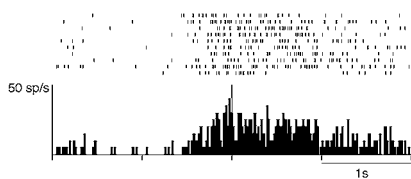
B) Experimenter sucks from a syringe



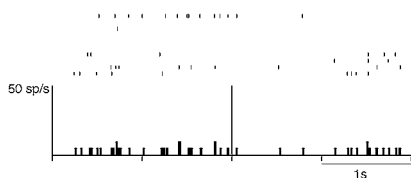
C) Experimenter mimes grasping food with the mouth



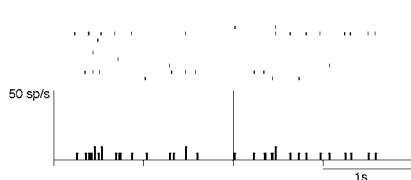
D) Monkey grasps food with the mouth



E) Monkey sucks from a syringe

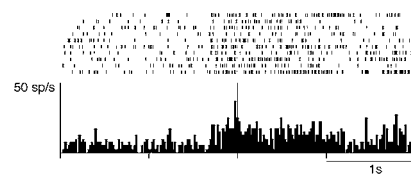


F) Food presentation

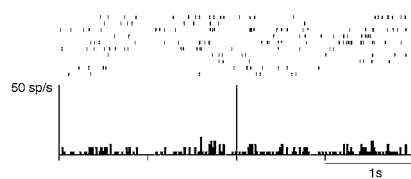


Neuron 15

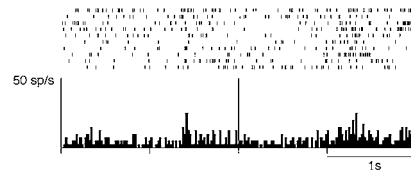
A) Experimenter sucks juice from a syringe



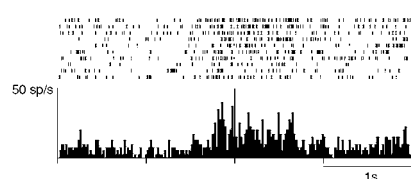
B) Experimenter grasps food with the mouth



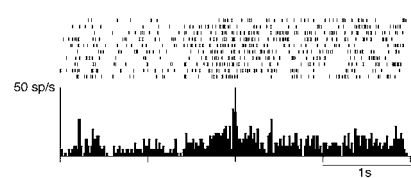
C) Experimenter mimes sucking



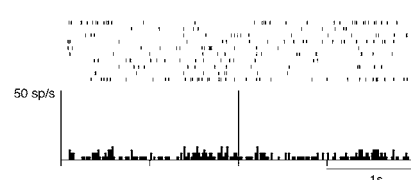
D) Monkey sucks from a syringe



E) Monkey grasps food with the mouth



F) Food presentation



time interval (1 s) centred at the alignment signal (500 ms before and 500 ms after) and compared (one-way ANOVA) to the background activity of that neuron before the action initiation (2000–1000 ms before alignment). A second analysis (two-way ANOVA, followed by Newman–Keuls *post hoc* tests comparisons) was then performed to compare the neuron activity in different experimental conditions. All analyses were performed with a significance criterion of $P < 0.05$.

Histological control

Histological control was made in monkey 1; monkey 2 is still alive. For detailed description of the histological processing, see Fogassi *et al.* (2001). Each animal was anaesthetized with ketamine hydrochloride (15 mg/kg i.m.) followed by an i.v. lethal injection of pentobarbital sodium and perfused through the left cardiac ventricle with buffered saline, followed by fixative. The brain was removed from the skull, photographed and then frozen and cut coronally. The sections (60- μ m thick) were stained using the Nissl method. The locations of penetrations were then reconstructed and related to the cytoarchitectonic areas of the ventral agranular cortex.

Results

Functional properties of mouth mirror neurons

In total, 485 neurons were recorded from area F5. A total of 412 were recorded from monkey 1 (right hemisphere) and 73 from monkey 2 (left hemisphere). All the recorded neurons, except 15 (3.1%), possessed motor properties. More specifically, 101 neurons (20.8%) discharged in association with active hand movements, 171 neurons (35.3%) in association with hand and mouth actions, and the remainder ($n = 198$) during mouth actions only (40.8%). The large prevalence of mouth-movement-related neurons is most likely due to the lateral location of the penetrations (see also below). Previous experiments showed that in this part of F5, mouth movements are mostly located (Gentilucci *et al.*, 1988; Godschalk *et al.*, 1995).

Out of 369 mouth-related neurons, 180 (48.7%) responded to visual stimuli. A set of them ($n = 130$, 35.2%) responded to the observation of mouth actions (monkey 1, $n = 104$; monkey 2, $n = 26$) while the remaining ($n = 50$, 13.5%) responded to other types of visual stimuli, such as object presentation or object motion. Neurons responding selectively to the observation of mouth actions will be referred to as 'mouth mirror neurons'. None of these neurons responded to the presentation of objects including food.

Seventy-nine mouth mirror neurons were studied long enough to assess quantitatively their properties. Sixty-seven (85%) responded to the observation of ingestive actions ($n = 41$ to a single action, $n = 26$ to two or more actions). Twelve (15%) responded to the observation of communicative actions ($n = 10$ to a single action; $n = 2$ to two actions). Note that in most neurons the response was clinically tested by more than one experimenter before quantitative data acquisition. During data acquisition one experimenter performed the actions in front of the

TABLE 1. Ingestive mouth mirror neurons subdivided according to the observed mouth actions effective in activating them

Category	Number of neurons
Grasping	19
Breaking	8
Sucking	6
Taking away	4
Others	4
Grasping/chewing	6
Grasping/breaking	7
Grasping/sucking	5
Grasping/holding	4
Others	4
Total	67

TABLE 2. Communicative mouth mirror neurons. For each neuron the effective observed and executed action are described

Effective observed action	Effective executed action
Lip-smacking	Sucking
Lip-smacking	Sucking and lip smacking
Lips protrusion	Grasping with lips
Lips protrusion	Lip smacking
Lips protrusion	Grasping and chewing
Tongue protrusion	Reaching with tongue
Tongue protrusion	Reaching with tongue
Tongue protrusion	Reaching with tongue
Tongue protrusion	Reaching with tongue
Teeth-chatter	Grasping
Lips/tongue protrusion	Grasping with lips and reaching with tongue
Lips/tongue protrusion	Grasping

monkey. We never found difference in neuronal discharge when the same gestures were made by different experimenters. Similarly, the specificity of the neuron response for the observed gesture was not affected by who was performing the gesture. Finally, although not systematically tested, we did not find any difference in the neuronal discharge when the gesture was performed with the experimenter facing the monkey or having his head directed toward other space locations. Table 1 shows the effective observed actions and the number of neurons responding to each of them.

Examples of 'ingestive' mouth mirror neurons are shown in Fig. 2. Neuron 68 responded to the observation of the experimenter grasping a piece of food with the mouth (A), but not to experimenter making other mouth actions (see B, sucking). No response was elicited by the observation of the experimenter miming the effective action (C). Similarly, no response was evoked by simple food presentation (F). The neuron strongly discharged when the monkey grasped a piece of food with its mouth (D), but not during other types of mouth actions (E, sucking).

Fig. 2. Example of two transitive mouth mirror neurons. In each panel, the rasters and the histograms represent the neuron response during a single experimental condition. The histogram represents the average of 10 trials. Rasters and histograms are aligned with the moment in which the mouth of the experimenter (observation conditions) or of the monkey (motor conditions) touched the food or when the food is abruptly presented (presentation conditions). During observation of mimed mouth grasping the alignment was made with the end of the movement. Ordinates, spikes/s; abscissae, time; bin width, 20 ms. Neuron 68, grasping with the mouth mirror neuron. (A) The experimenter approaches with his mouth the food held on a support and grasps it with the teeth; (B) the experimenter approaches with his mouth a juice filled syringe, held on a support, and sucks the juice; (C) the experimenter makes the same approaching and grasping movements as in (A), but no food is present; (D) the experimenter moves a piece of food to the monkey's mouth; the monkey grasps it with its teeth and eats it; (E) the experimenter moves a syringe filled with juice to the monkey's mouth; the monkey closes its lips and the teeth on the syringe and sucks; (F) the experimenter introduces abruptly a piece of food held on a stick in the monkey visual field and then keeps it still. In all observation conditions the stimulus was presented at about 75 cm from the monkey. Neuron 15, sucking mirror neuron. (A) the experimenter approaches with his mouth a juice filled syringe, held on a support, and sucks the juice; (B) same condition as in neuron 68 (A); (C) the experimenter makes the same approaching and sucking movements as in (A), but no syringe is present (D) the experimenter moves a syringe filled with juice to the monkey's mouth; the monkey closes its lips and the teeth on the syringe and sucks; (E) same condition as in neuron 68 (D); (F) the experimenter introduces abruptly a juice filled syringe held on a support in the monkey visual field and then keeps it still.

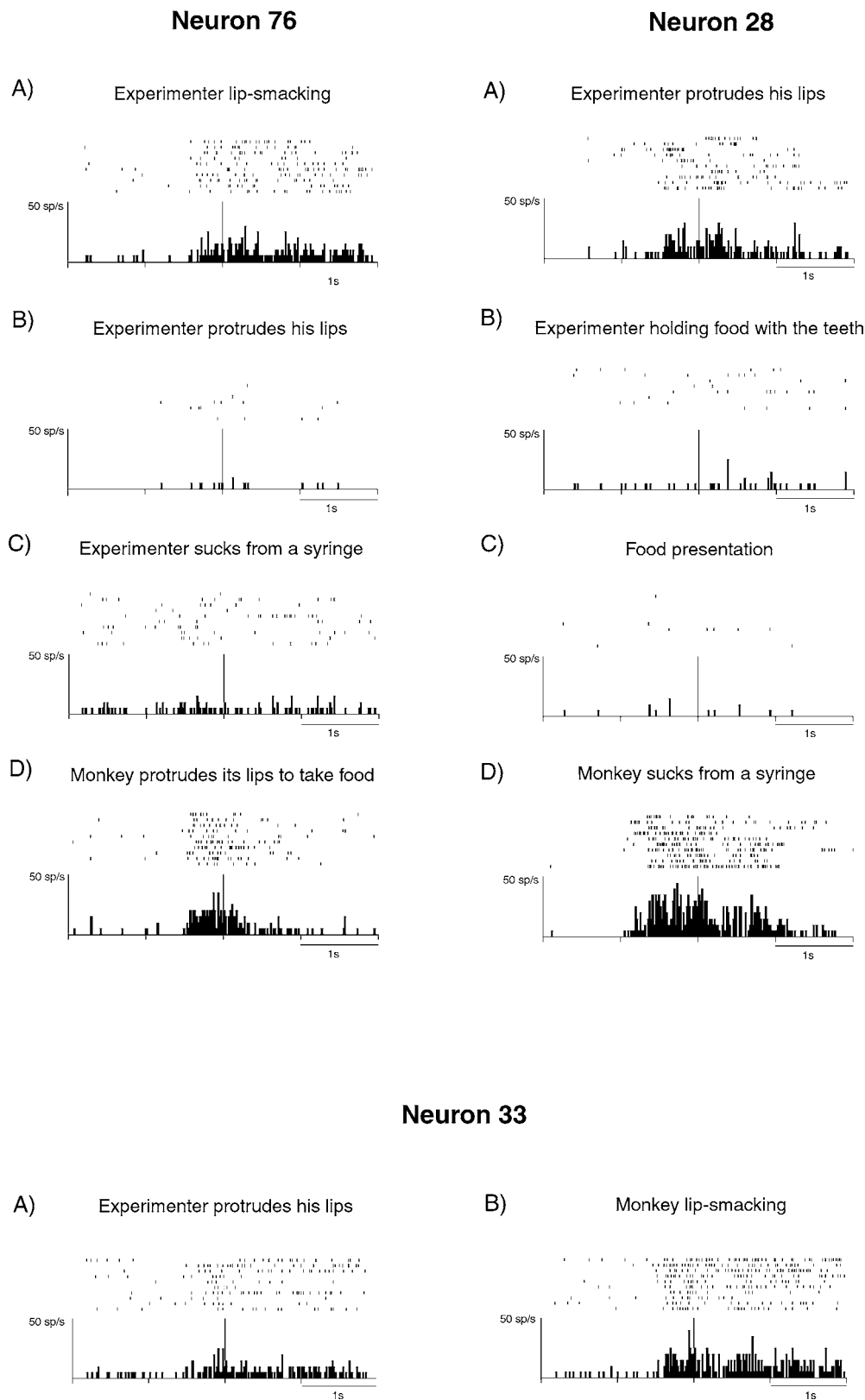


FIG. 3. Example of three intransitive mouth mirror neurons. During observation of intransitive actions the rasters and histograms alignment was made with the moment in which the action was fully expressed. For alignment during other experimental conditions see legend of Fig. 2. Neuron 76, lip smacking mirror neuron. (A) The experimenter makes a lip-smacking action looking at the monkey; (B) the experimenter protrudes his lips looking at the monkey; (C) same conditions as in neuron 68 (B); (D) the experimenter moves a piece of food to the monkey's mouth; the monkey protrudes its lips and takes the food. Neuron 28, lips protrusion mirror neuron. (A) The experimenter protrudes his lips looking at the monkey; (B) the experimenter approaches with his mouth a piece of food held on a support, then grasps and holds it with his teeth; (C and D) same conditions as in neuron 68 [(F) and (E), respectively]. Neuron 33, lips protrusion mirror neuron. (A) The experimenter protrudes his lips looking at the monkey; (B) during the experimenter lips protrusion the monkey respond almost simultaneously to the experimenter gesture by making a lip smacking action.

Monkey responses to human facial gestures

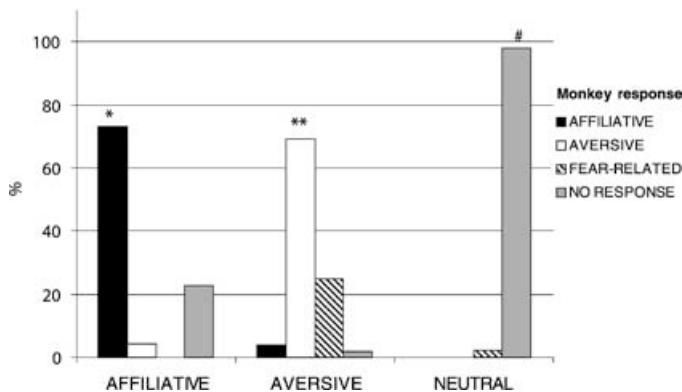


FIG. 4. Histograms showing the percentage of each category of monkey behavioural response to the different experimenter communicative facial gestures. Experimental details: nine monkeys (*Macaca nemestrina*), aged from 4 to 14 years, were used. The experimenter seated in front of the monkey cage with a neutral face. Then he performed the following facial gestures, one at the time, in a random order: lip smacking, lips protruded face, open mouth threat, neutral face. These gestures were performed staring at the monkey and were held for three seconds. Each gesture was presented to the monkey five times in two experimental sessions run in two different days. The experiment was recorded by a video camera and videotapes were subsequently analysed independently by two experimenters. Beginning of the trial was considered the moment in which the experimenter began a gesture. We analysed the monkey behavioural responses within five seconds from the beginning of the trial. A trial was considered valid if the monkey engaged its gaze with experimenter face. Single asterisk (*) indicates that affiliative responses were significantly more frequent than both aversive and fear-related responses ($P < 0.05$, paired t -test); double asterisk (**) indicates that aversive responses were significantly more frequent than both affiliative responses and no responses ($P < 0.05$, paired t -test). #Indicates that no responses were significantly more frequent than all the other behavioral responses ($P < 0.05$, paired t -test).

Neuron 15 responded to the observation of the experimenter sucking juice from a syringe (A) but not to experimenter making other mouth actions such as grasping with the mouth (B). No response was elicited by the observation of the experimenter miming the effective action (C). Similarly, no response was evoked by simple syringe presentation (F). The motor response of this neuron was less specific than that of neuron 68. Neuron 15 strongly discharged when the monkey sucked juice from the syringe with its mouth (D), but a discharge was present also when it grasped food with its mouth (E).

Examples of 'communicative' mouth mirror neurons are shown in Fig. 3. Neuron 76 responded specifically to the observation of lip-smacking (A). This neuron did not discharge when the experimenter performed other mouth actions such as, for example, 'lips protruded face' (B), an affiliative gesture in which protrusion of the lips is the main movement component (see Fig. 1). No response was evoked by the observation of ingestive actions (C). However, the neuron became active when the monkey grasped the food with the mouth requiring a slight protrusion of the lips and of the tongue (D). Mouth grasping without lips protrusion was not effective.

Neuron 28 responded specifically to the observation of the experimenter protruding his lips (A). The observation of an ingestive action such as the experimenter holding food between his teeth did not evoke any discharge (B). Similarly, no response was elicited by object or food presentation (C). On the motor side, this neuron, as the previous one, discharged during an ingestive action, namely when the monkey sucked juice from a syringe (D).

Similar to the hand mirror neurons (Gallese *et al.*, 1996), most (95%) ingestive mouth mirror neurons showed a clear correspondence

between the effective observed and the effective executed action. In 37% of the neurons the effective observed and executed actions were the same (strictly congruent neurons). In 58% of the neurons the effective observed and executed actions were visually or functionally similar (broadly congruent neurons). Examples of broadly congruent neurons are neurons that code motorically a single action (e.g. grasping with the mouth) while visually, in addition to that action, other mouth actions (e.g. breaking).

More complex was the relation between the observed and executed action in communicative mouth mirror neurons. All of them but one discharged when the monkey performed specific ingestive actions. In general, there was a good correlation between the motor features of the effective observed (communicative) action and those of the effective executed (ingestive) action (Table 2). For example, when a neuron discharged to the observation of lips protrusion, its motor response occurred during the monkey lips protrusion for getting juice and not during other ingestive actions, while when the visual response was elicited by tongue protrusion, reaching with the tongue was the most effective executed action.

During the recording of two neurons that responded to communicative gestures, we were able to evoke an active communicative action. For one of these neurons, the effective observed gesture was lip-smacking, for the other lips protrusion. Figure 3 (lower panel) illustrates the responses of this last neuron (neuron 33). In Fig. 3A, the monkey observed the experimenter protruding the lips and maintaining them then protruded. The synchronisation bar indicates the end of the dynamic phase of the movement. The neuron's discharge clearly correlated with the experimenter's gesture. In Fig. 3B, the experimenter made the same action, but this time the monkey responded by lip smacking. Note the increase of the discharge in comparison with Fig. 3A and its rhythmic character. This neuron did not discharge when the monkey sucked juice from a syringe or when it grasped a piece of food with the hand (not shown in the figure).

Control experiments

Ethological data

The finding of neurons that respond selectively to the observation of communicative gestures made by the experimenter suggests that the monkeys observing them were able to recognise the different gestures in spite of the fact that they were made by a non-conspecific. To assess this, a behavioural experiment was carried out. Nine monkeys were used. An experimenter, standing in front of the monkey, free in its cage, performed affiliative (lip-smacking, lips protruded face) and aversive (open mouth threat) gestures. As a control, the experimenter looked at the monkey without showing any emotion (neutral face). A total of 168 responses were analysed, subdivided into affiliative, aversive, fear related and no response. The results are presented in Fig. 4. Affiliative gestures performed by the experimenter ($n = 71$) evoked in the monkey significantly more affiliative responses ($n = 52$, 73.0%) than aggressive ($n = 3$, 4.0%) and fear-related ($n = 0$) responses ($P < 0.05$, paired t -test). In 16 (22.0%) cases monkeys did not make any response. Threatening facial gestures ($n = 52$) evoked significantly more aggressive ($n = 36$, 69.0%) or fear-related ($n = 13$, 25%) responses than affiliative responses ($n = 2$, 4%, $P < 0.05$, paired t -test). Neutral face ($n = 45$) virtually never evoked a monkey response.

EMG recordings

Figure 5 (upper part) shows the EMG recordings from human and monkey face muscles while the experimenter performed ingestive actions (grasping with the mouth and sucking) in front of the monkey. It is clear that the observation of experimenter's actions did not elicit

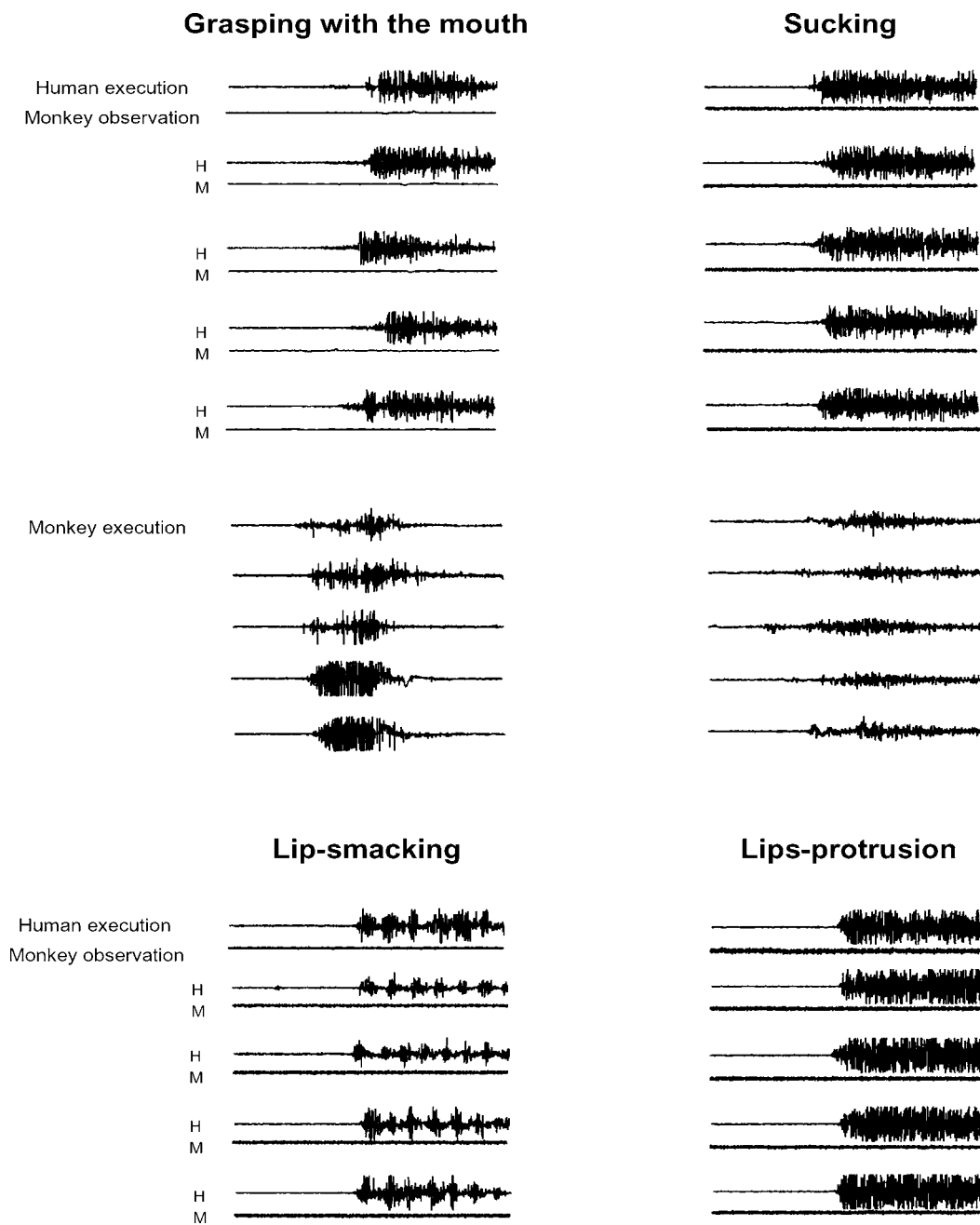


FIG. 5. Left upper part. EMG recording of the experimenter and monkey masseter muscle. Left upper panels: in each trial the EMG during experimenter execution (H) and monkey observation (M) of the gesture is recorded. During the action the experimenter approaches with his mouth to the food held on a support and grasps it with the teeth. Left lower panels: EMG recording of the monkey masseter muscle during execution of a grasping with the mouth action. Right upper part. EMG recording of the experimenter and monkey orbicularis oris muscle. Right upper panels: in each trial the experimenter approaches with his mouth a juice filled syringe, held on a support, and sucks the juice. Right lower panels: EMG recording of the monkey orbicularis oris muscle during the execution of a sucking action. In each trial the experimenter moves a syringe filled with juice toward the monkey's mouth; the monkey closes its lips and the teeth on the syringe and sucks. Left lower part. EMG recording of the experimenter and monkey orbicularis oris muscle. In each trial the experimenter makes a lip smacking gesture looking at the monkey. Right lower part. EMG recording of the experimenter and monkey orbicularis oris muscle. In each trial the experimenter makes a pucker (lips protrusion) gesture looking at the monkey. Five trials were recorded for each execution and observation condition. Each trial lasts 2 s.

any activation of the monkey's face muscles. The lower panels of the upper part show, as a control, the activity of the same face muscles when the monkey actively performed the two gestures.

Figure 5 (lower part) shows the EMG recordings during the execution by the experimenter of two communicative gestures (lip-smacking and lips protrusion). Also in this case no EMG response was evident in the recorded monkey muscles. As already mentioned, the monkey

produced a communicative gesture in response to that of the experimenter only rarely. Although no other facial muscles were recorded, the absence of EMG activation in muscles specifically involved in the observed actions makes it unlikely that other muscles involved in these actions may have been activated.

For each action, 10 trials were presented to the monkey. The results were the same as those presented in the figures.

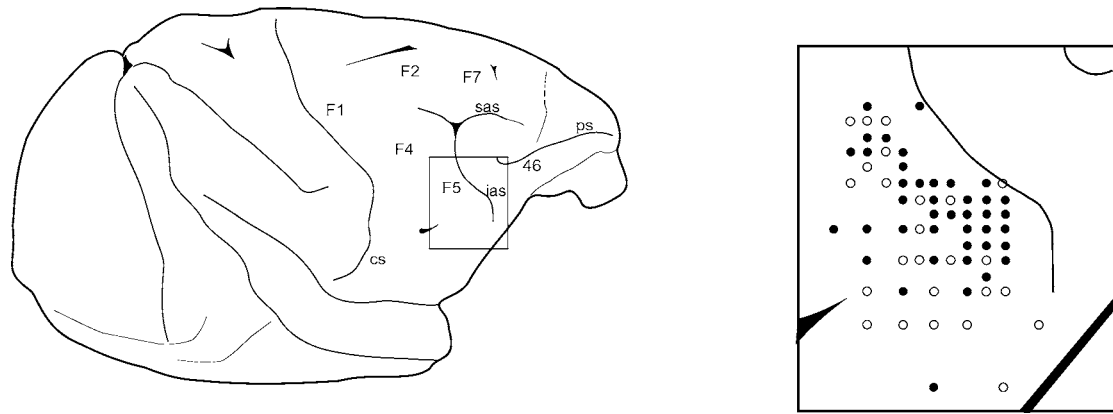


FIG. 6. Left side: Lateral view of the right hemisphere of monkey 1. The rectangle, enlarged on the right side, delimits the part of the ventral premotor cortex explored in the present study. For the classification of the areas of the agranular frontal cortex see Matelli *et al.* (1985). Abbreviations: cs, central sulcus; ias, inferior arcuate sulcus; ps, principal sulcus; sas, superior arcuate sulcus. Right side: reconstructed view of the penetrations performed in area F5. Filled circles: penetrations in which mouth mirror neurons were recorded. Empty circles: penetrations in which no mouth mirror neurons were found.

Eye movements

In order to ascertain whether the monkeys observed the different type of actions used in the experiment, their ocular behaviour was video-recorded as described in Materials and methods. The results showed that typically the monkey shifted its gaze toward the mouth of the experimenter and gazed at it for an average of 650 ms. Monkey 3 gazed at ingestive actions in 92% of trials and at communicative actions in 97.5% of trials. The percentages for monkey 4 were 80% for both types of actions. In general, for ingestive actions the monkeys kept their eyes fixed on the experimenter both during the opening and closure of his mouth until the food (or the syringe) was in contact with it. In the case of sucking and reaching with the tongue monkey 3 tended to perform several (two to four) gazes instead of a single, continuous gaze. Among the four communicative actions, three (lips protrusion, tongue protrusion and open mouth) consisted of a dynamic phase followed by a prolonged static phase in which the mouth gesture was maintained. During the presentation of these gestures both the monkeys started to look at the experimenter at the beginning of the mouth movement and kept their gaze fixed on his mouth for about 400 ms (average 425.5 ms). During lip smacking, a rhythmic communicative action, the monkeys typically observed several (at least the first three) mouth opening-closure alternations.

Histology

Histological control of the microelectrode tracks showed that most of the penetrations were located in the lateral part of F5 (Fig. 6). Almost all mouth mirror neurons were found in the convexity of the lateral part of area F5. More than 85% of them were found at a depth ranging from 200 to 1500 μm (Fig. 7). Figure 8 shows an example of a coronal section taken through the recorded region reporting the depth at which various mouth mirror neurons were found (filled squares).

Discussion

Mouth mirror neurons: basic findings and control experiments

Understanding actions made by others is a fundamental cognitive capacity on which depends social behaviour. Although various hypotheses (not necessarily mutually exclusive) have been advanced to explain action recognition (Barresi & Moore, 1996; Rizzolatti *et al.*, 2001), one that attracted considerable attention in recent years is the 'direct matching hypothesis'. According to this hypothesis an action

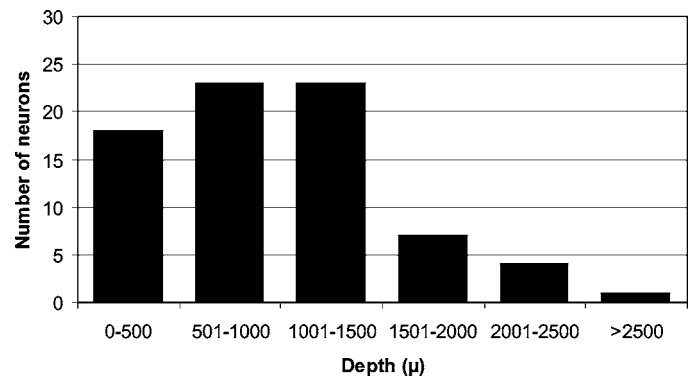


FIG. 7. Histograms showing the number of mouth mirror neurons found at different depth intervals in the recorded sector of area F5.

made by another individual is understood when its observation activates the corresponding observer's motor representation. Because individuals know the outcome of their motor representations, when their motor representations are activated the meaning of actions made by others are understood (Rizzolatti *et al.*, 2001; for evidence in favour of the existence of a visuo-motor coupling mechanism see also Iacoboni *et al.*, 1999; Bekkering & Wohlschlaeger, 2002; Prinz, 2002; Viviani, 2002).

The neurophysiological basis of the direct matching hypothesis is the presence in the monkey premotor cortex of neurons that discharge when the monkey performs a specific action and when it observes a similar action performed by another individual ('mirror neurons', Gallese *et al.*, 1996; Rizzolatti *et al.*, 1996). The studies of mirror neurons concerned up to now mostly or exclusively the functional properties of hand mirror neurons. This is true for the earlier studies cited above as well as for recent studies in which more complex functional properties of mirror neurons were investigated such as their capacity to recognise actions on the basis of their sound (Kohler *et al.*, 2002) or to 'deduce' their meaning on the basis of limited visual cues (Umiltà *et al.*, 2001).

The purpose of the present experiments was to study the responses of F5 neurons motorically coding mouth actions to the observation of mouth actions made by another individual. The results showed that 35% of mouth motor neurons discharged when the monkey observed mouth actions (mouth mirror neurons). The majority of mouth mirror

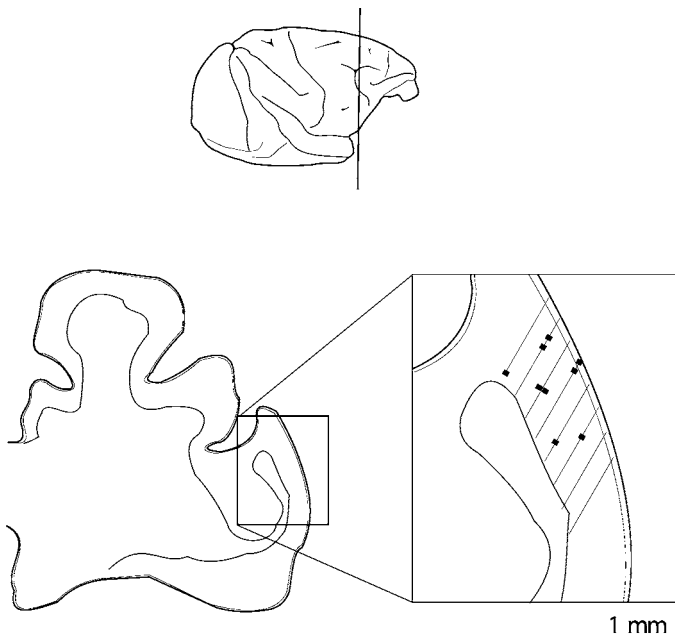


FIG. 8. Example of a coronal section taken through the recorded area of monkey 1. Top: lateral view of the right hemisphere indicating the level of the coronal section shown in the bottom part of the figure. Bottom: coronal section and enlarged view (right) of the convexity of F5 showing eight penetrations traces. The depth at which mouth mirror neurons were found are marked with filled squares.

neurons (85%) discharged during the observation of ingestive mouth actions, others (15%) during the observation of communicative actions.

Control experiments showed that the mirror effect was not due to spurious effects such as mouth or face movements concurrent to action observation. The idea that monkeys imitate the observed movements is a diffuse prejudice. Ethological studies, however, contradict this contention and show that, unlike apes, the monkeys do not copy the actions made by others (see Visalberghi & Frigaszy, 1990; Byrne, 1995; Tomasello & Call, 1997). This finding was confirmed in the present experiment by the observation of monkeys' behaviour while they looked at the actions made by the experimenters and by recording the EMG from their face and mouth muscles in the same condition. In accord with previous data obtained during the observation of hand action (Gallese *et al.*, 1996), no evidence whatsoever was found that the monkeys performed face or mouth movements in response to experimenters' ingestive actions (for communicative actions see below). Tongue movements were not recorded, but it is hard to believe that tongue movements would have occurred alone, not in synergy with face and mouth movements, during the observation of facial and mouth actions. Furthermore, the general organization of F5 for both hand and mouth movements is in terms of actions and not individual movements (see Jeannerod *et al.*, 1995; Rizzolatti *et al.*, 2000; Rizzolatti & Luppino, 2001).

Area F5 controls oro-facial and hand movements, but not eye movements (Kohler *et al.*, 2002). Thus, the possibility that the neuron discharge during action observation could be due to eye movements can be ruled out on the basis of the general properties of F5 neurons and the good congruence between the observed action and the action that triggered the neurons when executed. While the eye movement interpretation of mirror response is obviously untenable, eye movements could have determined a bias in the type of the recorded mirror neurons. If, for example, ingestive actions attracted more monkey's

attention than communicative gestures, the monkey could fixate the former and not the latter. Lack of fixation could, in turn, decrease the salience of the observed stimuli and prevent the neuron from discharging. The same logic could be applied to the different classes of ingestive actions. Some could have been fixated and thus have produced a neuron response, others could have been neglected. The results of eye movement recordings allowed us, however, to discard all these possibilities. The monkeys fixated all actions and there was no evidence that the amount of neurons belonging to different classes depended on the monkey's interest in the observed action.

Ingestive mouth mirror neurons

The functional properties of ingestive mouth-mirror neurons are very similar to those of hand mirror neurons. As hand mirror neurons, mouth mirror neurons require an interaction between an effector and an object in order to be triggered. The presentation of an object alone or of a not goal-directed movement is insufficient to activate the neurons. Finally they show congruence between the effective observed and the effective executed action. These findings extend the previous concept of the mirror system as a system matching action observation and action execution from hand to mouth actions.

Brain imaging experiments provide evidence of a mirror neuron matching system also in humans (Iacoboni *et al.*, 1999; Nishitani & Hari, 2000, 2002). A recent fMRI experiment strongly suggests that such a system exists in humans also for ingestive mouth actions (Buccino *et al.*, 2001). Normal volunteers were instructed to observe different types of mouth actions such as biting and chewing. The results showed that the observation of these actions activates bilaterally the posterior part of the inferior frontal gyrus centred on the pars opercularis (area 44) and extending to the pars triangularis (area 45) and to ventral area 6 (Buccino *et al.*, 2001). Interestingly, area 44 is considered, on the basis of anatomical and functional criteria, to be the homologue of monkey's area F5 (Von Bonin & Bailey, 1947; Petrides & Pandya, 1994; see also Rizzolatti & Arbib, 1998).

Communicative mouth mirror neurons

More intriguing are the properties of the second set of F5 mouth mirror neurons, the communicative neurons. These neurons have characteristics that differentiate them both from ingestive mirror neurons and the previously studied hand mirror neurons.

First of all, communicative mirror neurons, unlike other mirror neurons, discharge in response to actions such as lip-smacking or tongue protrusion, actions that are not object-directed. A possible objection to this is that the response of the neuron to the presented stimulus is, actually, not to the stimulus as it visually appears. It might be that, during the observation of an intransitive action, the monkey reconstructs internally a goal-directed action. For example, in the case of tongue protrusion, this intransitive action would evoke in the observing monkey the idea of licking. Thus, the perceived action is not perceived as an intransitive communicative gesture (or a fragment of it) but as a transitive ingestive action.

Recent findings showed that indeed, under certain circumstances, the monkey could complete an action and treat an action that from its observation point of view was intransitive as a goal directed action. Umiltà *et al.* (2001) showed that hand mirror neurons that do not discharge when a movement is not directed toward an object, become active when the observed action is directed toward a hidden object, provided that the monkey knows that a hidden object exists. In hidden condition the monkey sees an intransitive action, but mentally transforms it into a transitive action. One might argue that a similar operation is at the basis of the response of communicative mouth mirror neurons or of some of them. This explanation, however, is hard

to reconcile with the fact that the response to the observation of actual ingestive action was absent or very weak in all neurons classified as communicative. In contrast, hand mirror neurons responding to 'hidden' actions typically show the strongest responses when the entire action is visible. Thus, although attractive for its unitary explanation of mirror effects in F5, this interpretation of communicative mirror neurons appears to be contradicted by their basic properties.

A second fundamental difference between communicative and the other mirror neurons (hand and ingestive mirror neurons) is that, unlike in the latter, in the former the effective motor action is not identical to the effective observed one. All studied communicative mirror neurons discharged during active ingestive actions made by the monkey. There are two problems here: a methodological problem and a conceptual one. The methodological problem is that we had difficulty to evoke routinely communicative gestures during neuron recordings. This prevented us to study satisfactorily the neuron response during the execution of these gestures. Thus, we know that for the neurons that we called communicative mirror neurons the best visual stimulus is a communicative stimulus, we know also that they discharge during ingestive actions, but we know very little about their behaviour during active communication. It is fundamental to stress, however, that in the two cases in which we elicited communicative gestures during neuron recording, there was a clear communicative motor counterpart. Thus, although any conclusion on this point can be only very tentative, we are inclined to think that the property to discharge during active communicative actions is not limited to the two above mentioned neurons but is rather a property of many, if not all, of them.

Why should ingestion and communication share a common neural substrate? Although the discovery of a link between communicative and ingestive actions in F5 was for us an unexpected finding, there are ethological and evolutionary data that strongly suggest that these two functions are strictly linked. Particularly important in this respect are the studies of Van Hooff (1962, 1967). According to this author the monkey communicative gestures (e.g. lip-smacking, lips protruded face) are ritualizations of ingestive actions that are used for affiliative purposes. The typical behavioural pattern of the lip-smacking, he writes "gives the impression that the animal is tasting the particle", which has been removed from the skin during a grooming session. "When one animal starts grooming another, the first groom-movements may be accompanied by a smacking that is not preceded by the act of bringing a particle into the mouth" (Van Hooff, 1962, 1967). In other words, the knowledge common to the communicator and the recipient of communication about food and ingestive action became the common ground for social communication. Ingestive actions are the basis on which communication is built.

In a rather similar vein, MacNeilage (1998) proposed that the human vocal communication derived from the cyclic open-close mandibular alternation originally evolved for food ingestion. According to this view monkey lip-smacking represents a communicative action that clearly shows its derivation from ingestive mouth movements. Syllables, which share with lip-smack similar movement dynamics, would represent a further evolution of the same basic mechanism.

The production of communicative signals in nonhuman primates has been traditionally associated to the activity of mesial cortical areas and subcortical structures (Jürgens, 1995; Jürgens, 2002), that is to structures whose activation is correlated to emotional behaviour. The limited amount of communicative neurons found in F5 is consistent with this view. Yet, their presence in an area that is not related to emotions, but to the expression/understanding of 'cold action' (not emotionally laden) may suggest that in the macaque there is an initial capacity to control and emit 'voluntarily' (not emotionally) social

signals mediated by frontal lobe. Finally, and most interestingly, this capacity develops in a cortical area that, in another primate evolutionary line, became a key area for verbal communication.

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