

Research report

Premotor cortex and the recognition of motor actions

Giacomo Rizzolatti^{*}, Luciano Fadiga, Vittorio Gallese, Leonardo Fogassi

Istituto di Fisiologia Umana, Università di Parma, Via Gramsci 14, I-43100, Parma, Italy

Accepted 22 August 1995

Abstract

In area F5 of the monkey premotor cortex there are neurons that discharge both when the monkey performs an action and when he observes a similar action made by another monkey or by the experimenter. We report here some of the properties of these 'mirror' neurons and we propose that their activity 'represents' the observed action. We posit, then, that this motor representation is at the basis of the understanding of motor events. Finally, on the basis of some recent data showing that, in man, the observation of motor actions activate the posterior part of inferior frontal gyrus, we suggest that the development of the lateral verbal communication system in man derives from a more ancient communication system based on recognition of hand and face gestures.

Keywords: Premotor cortex; Mirror neuron; Gesture recognition; Broca's area; Movement representation

1. Introduction

An important discovery of the last years was that the monkey agranular frontal cortex is functionally subdivided into several different areas [10,11,19,24,27,28,33–35,37,38,54]. Among them one –area F5– is particularly interesting for its complex properties and for its possible homology with Broca's area of human brain [2,15,42].

F5 is located in the ventro-rostral part of area 6, just caudal to the lower arm of the arcuate sulcus. Stimulation and recording experiments showed that this area is related to hand and mouth movements [20,24,52,55]. F5 has a rough somatotopic organization. Hand movements are represented mostly in its dorsal part, while mouth movements tend to be represented ventrally.

While little is known about the properties of F5 neurons related to mouth movements, the properties of those controlling hand movements were extensively studied. Hand-movement F5 neurons have both motor and sensory properties. As far as the motor properties are concerned, two are their main characteristics. Firstly, most neurons discharge selectively during particular goal-related hand movements such as grasping, holding, manipulating. Secondly, many of them are specific for particular types of hand prehension, e.g. precision grip, finger prehension,

whole hand prehension. For the sensory properties, the most interesting aspect is that a considerable part of F5 neurons fire at the presentation of 3D objects, in the absence of any overt movement. In many cases the discharge occurs only if there is a match between the object size and the type of grip coded by the neuron [22,52].

F5 receives a strong input from the inferior parietal lobule [6,31,47] and, in particular, from area AIP [16,22,32], an area located in the lateral bank of the inferior parietal sulcus rostral to the oculomotor area LIP. As in the case of F5, a large number of neurons in AIP are related to hand movements, the large majority preferring specific types of hand grip [57,58]. About 40% of AIP neurons discharge during the appropriate hand movement both in darkness or in the light (motor dominant neurons). The remaining neurons discharge stronger (visual and motor neurons) or exclusively (visual dominant neurons) in the light. A part of neurons of these last classes become active when the monkey fixates an appropriate object remaining still and without being required to make a movement toward it.

Taken together, these data indicate that AIP and F5 form a cortical circuit which transforms visual information on the intrinsic properties of the objects into hand movements that allow the animal to interact appropriately with the objects. Motor information is then transferred to F1, to which F5 is directly connected, as well as to various subcortical centers for movement execution [22].

^{*} Corresponding author. Fax: (39) (521) 291-304.

Recently we discovered that a particular subset of F5 neurons, which from the motor point of view are undistinguishable from the rest of the population, discharge when the monkey observes meaningful hand movements made by the experimenter ('mirror neurons') [9]. The effective experimenter's movements included, among others, placing or taking away objects from a table, grasping food from another experimenter, manipulating objects. There was always a link between the effective observed movement and the effective executed movement.

These data suggest that area F5 is endowed with an observation/execution matching system. When the monkey observes a motor action that belongs (or resembles) its movement repertoire, this action is automatically retrieved. The retrieved action is not necessarily executed. It is only represented in the motor system. We speculated that this observation/execution mechanism plays a role in understanding the meaning of motor events [9,22].

The main aim of the present article is to discuss this proposal, taking into consideration some recent data showing that an observation/execution matching system does exist in man [13] and that the cortical region involved in this matching is a part of the region usually referred to as Broca's area [53]. Since this article means to be essentially a theoretical article, in the Results section we will present only a description of the most important features of 'mirror' neurons and will show some examples of them. A detailed description of these neurons and all the control experiments (e.g. EMG recordings, recordings from F1 neurons) that we performed in order to exclude that 'mirror' effect could be due to monkey's movements or other spurious factors will be presented elsewhere.

2. Materials and methods

2.1. Recording

Single neurons were recorded from two unanesthetized, behaving monkeys (*Macaca nemestrina*). 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.

The surgical procedures for neuron recordings were the same as previously described [17,54]. The head implant included a head holder and a chamber for single-unit recordings. Neurons were recorded using tungsten microelectrodes inserted through the dura which was left intact. Neuronal activity was amplified and monitored on an oscilloscope. Individual action potentials were isolated with a time-amplitude voltage discriminator. The output signal from the voltage discriminator was monitored and fed to a PC for analysis.

2.2. 'Clinical' testing and behavioral paradigm

All neurons were first informally tested by showing the monkey objects of different size and shape, and by letting him grasp them (for details see [17,52]). Every time a neuron became active during the monkey's hand movements, its properties were studied in a behaviorally controlled situation. A testing box was placed in front of the monkey. The box front door was formed by a one-way mirror. The room illumination was such that the monkey could not see inside the box during intertrial periods.

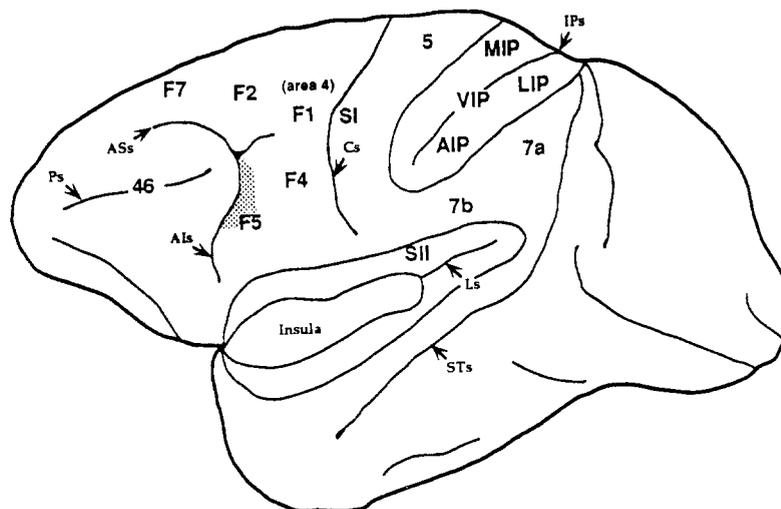
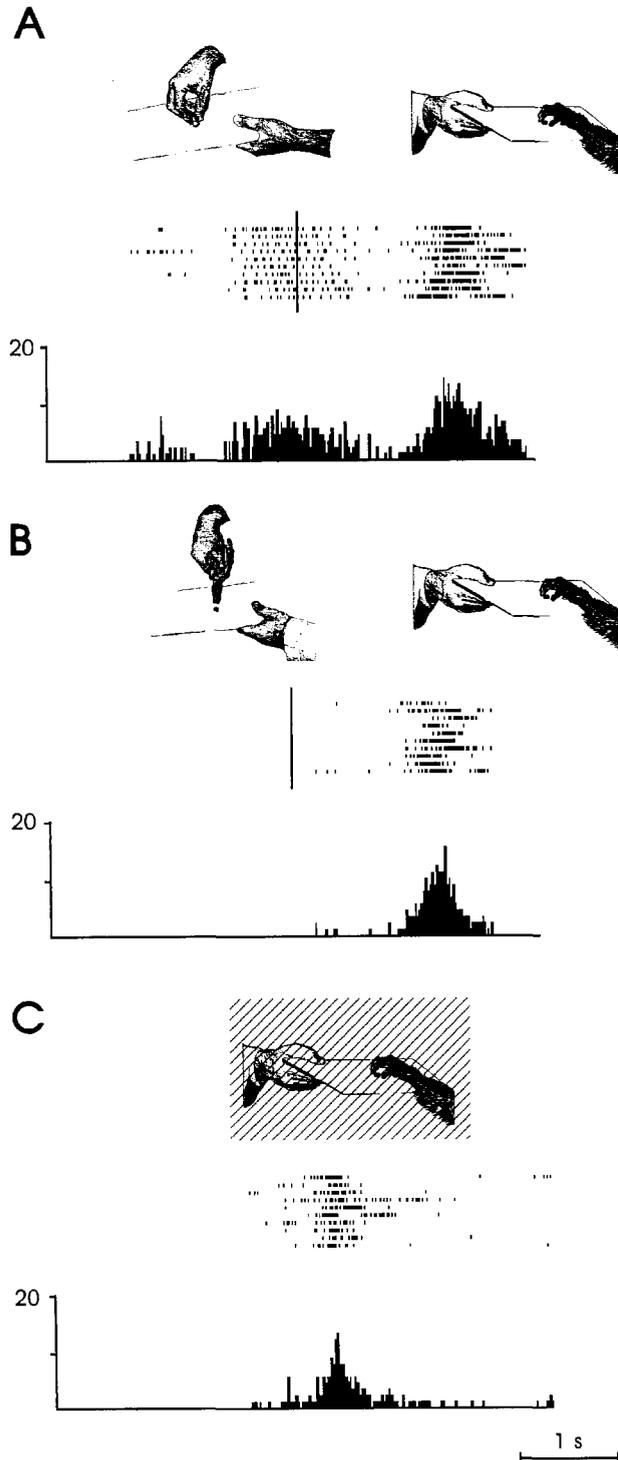


Fig. 1. Lateral view of the monkey brain. The shaded area shows the anatomical localization of the recorded neurons. Frontal agranular cortical areas are classified according to Matelli et al. [33]. Abbreviations: AIP, anterior intraparietal area; Als, inferior arcuate sulcus; ASs, superior arcuate sulcus; Cs, central sulcus; IPs, intraparietal sulcus; LIP, lateral intraparietal area; Ls, lateral sulcus; MIP, medial intraparietal area; Ps, principal sulcus; SI, primary somatosensory area; SII, secondary somatosensory area; STs, superior temporal sulcus; VIP, ventral intraparietal area. Note that IPs and Ls have been opened to show hidden areas.

Geometric solids of different size and shape were placed inside the box. The monkey started each trial by pressing a switch. Switch lit the box and made the object visible. After a delay of 1.2–1.5 s, the box front door opened, thus allowing the monkey to reach for and grasp the object. The

animal was rewarded with a piece of food located in a well under the object. Arm and hand movements were recorded using a computerized movement recording system (ELITE System, see [14]). This system consists of two infrared TV-cameras and a processor which elaborates the video images in real time and reconstructs the 3D position of infrared reflecting markers. The markers used for reconstructing the monkey's hand and arm movements were placed on the first phalanges of the thumb and the index finger and on the radial apophysis.



2.3. Testing of 'mirror' properties

'Mirror' properties were tested by performing a series of motor actions in front of the monkey. These actions were related to food grasping (e.g. 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 manipulation of food or other objects (e.g. breaking, tearing, folding), or were intransitive gestures (non-object related) with or without 'emotional' content (e.g. threatening gestures, lifting the arms, waving the hand, etc.).

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, pincers); 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 (50 cm, 1 m and 2 m).

The animal's behavior 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 behavior or the experimenters' actions to the neuron's discharge. When possible, response histograms were also constructed using a contact detecting circuit for aligning behavioral events and neuron's discharge.

Fig. 2. Visual and motor responses of a mirror neuron. The behavioral situations are schematically represented in the upper part of each panel. In the lower part are shown a series of consecutive rasters and the relative peristimulus response histograms. A, the experimenter grasps a piece of food with his hand and moves it towards the monkey who, at the end of the trial, grasps it. The neuron discharges during grasping observation, ceases to fire when the food is moved and discharges again when the monkey grasps it. B, the experimenter grasps the food with a tool. Subsequent sequence of events as in A. The neuron response during action observation is absent. C, the monkey grasps food in the darkness. In A and B the rasters are aligned with the moment in which the food is grasped by the experimenter (vertical line across the rasters). In C the alignment is with the approximate beginning of the grasping movement. Histogram bin width: 20 ms. Ordinates, spikes/bin; abscissae, time.

2.4. Histological identification

After the last experiment the animal was anesthetized with ketamine (15 mg/kg, 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 [33]). The animal was then placed in the stereotaxic apparatus, the dura was removed, and the stereotaxic coordinates of the arcuate and central sulci were assessed. The brain was blocked coronally on a stereotaxic 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 [33].

3. Results

Fig. 1 shows a lateral view of the monkey brain. ‘Mirror neurons’ were recorded from the dorsal convexity of the cortex (shadowed area) and the adjacent posterior bank of the arcuate sulcus. Both these cortices are part of area F5. Mirror neurons represented, approximately, 20% of the recorded neurons ($n = 300$).

With the term ‘mirror neurons’ we indicated those neurons that became active when the monkey observed meaningful hand actions performed by the experimenter. The simple presentation of objects, even when held by hand, did not evoke the neuron discharge. The majority of mirror neurons (about 60%) were selective for one type of action (e.g. grasping). Some were highly specific, selectively firing during the observation of a particular type of hand configuration used to grasp or manipulate an object (e.g. precision grip, but not whole hand prehension). The remaining neurons were activated by the observation of two or more hand actions. The actions most represented were: grasp, put object on a surface in front of the monkey, manipulate.

A typical example of a mirror neuron is presented in Fig. 2. In Fig. 2A (left part) the monkey observes the experimenter grasping a small piece of food placed on a tray. The tray is then moved towards the monkey and the monkey grasps the food (right part). The neuron discharges when the experimenter grasps the food, stops firing when the food is moved towards the monkey, and discharges again when the monkey grasps the food. In Fig. 2B the experimenter grasps the food using a tool, then, as in Fig. 2A, gives the food to the monkey. In this case there is no response during action observation. The neuron fires only during monkey’s grasping.

The discharge pattern illustrated in Fig. 2A is typical of mirror neurons. Note that there was no response when food was moved toward the monkey and became therefore

available to him. This absence of response just before the actual movement allows one to rule out motor preparation as a possible explanation for the neuron’s activation during grasping observation.

The interaction between hand and object (Fig. 2A) was

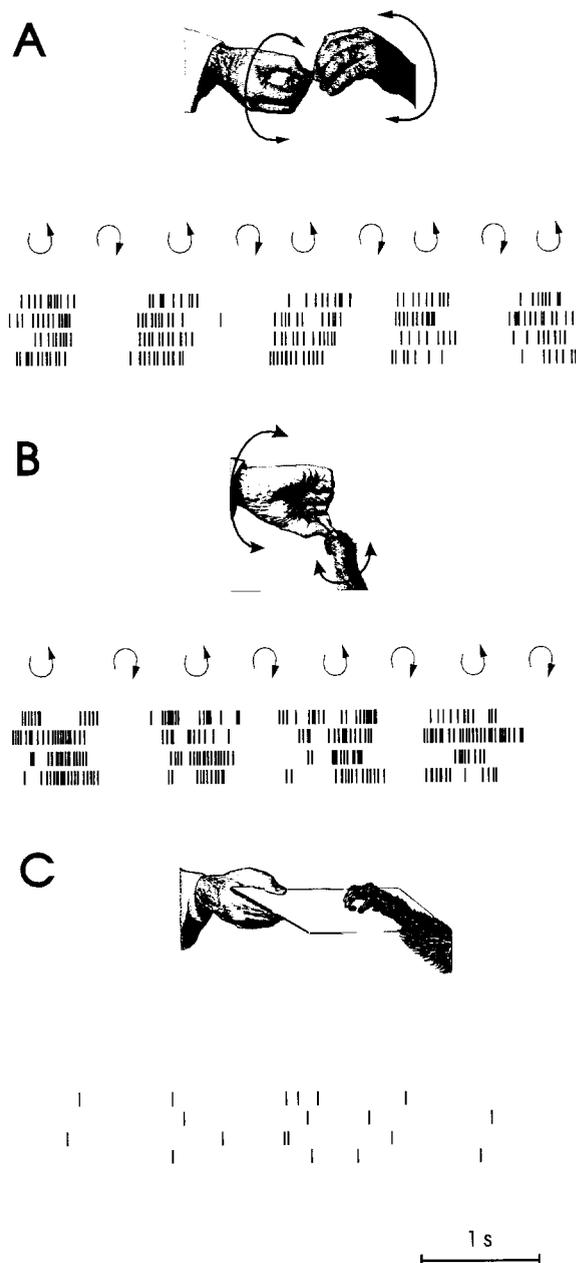


Fig. 3. Example of a highly congruent mirror neuron. A, the monkey observes the experimenter who rotates his hands around a raisin in opposite directions alternating clockwise and counterclockwise movements. The response is present only in one rotation direction. B, the experimenter rotates a piece of food held by the monkey who opposes the experimenter movement making a wrist rotation movement in the opposite direction. C, monkey grasps food using a precision grip. Four continuous recordings are shown in each panel. Small arrows above the records indicate the direction of rotations.

a fundamental requisite for neuron activation. Hand movements performed without an object did not activate the neurons. This was usually true also when food was grasped with a tool (Fig. 2B). In this last situation only few neurons became active and, in most cases, much less than during hand movements. Covering the object with a container (e.g. a beaker), with a cardboard, or removing it from the monkey's view together with the surface on which it was located did not activate mirror neurons.

The great majority of mirror neurons (79%) had also motor properties. The possibility that the discharges associated with active movements were due to the monkey's vision of his own hand was controlled by recording neuron activity during grasping made in darkness. All neurons were found to be active in this condition. Fig. 2C illustrates this finding.

A comparison carried out in each mirror neuron between the effective visual stimuli and the effective active movements, showed the presence of different degrees of congruence. A very high degree of congruence was found in those neurons that, being highly specific in their motor properties, were also highly specific in their visual properties. In these neurons the action coded in motor terms coincided with the action that, when seen, triggered the neuron.

The activity of a highly congruent mirror neuron is illustrated in Fig. 3. This neuron discharged when the experimenter rotated his hands in opposite directions around a small piece of food, as if for breaking it (Fig. 3A). Neither the observation of grasping movements, nor

active grasping (Fig. 3C) triggered the neuron. When the monkey made wrist rotations in order to take away the food from the experimenter's hand, a brisk response appeared (Fig. 3B).

Another example of a congruent neuron is illustrated in Fig. 4. Also in this case the only visual stimulus capable to activate the neuron was the observation of an action similar to that coded by the neuron. Fig. 4A shows that the observation of the experimenter placing a piece of food on a tray did not modify the discharge rate of the neuron. The discharge, however, was strongly inhibited during the observation of the experimenter grasping the same piece of food (Fig. 4B). The neuron's discharge was also strongly inhibited when the monkey grasped the food (Fig. 4C).

A broader type of congruence between the observed and the executed action was found in those neurons which could be activated by several visually related observed actions (such as different types of prehension or different actions such as placing and grasping) beside the one corresponding to the monkey's effective movement. Only few neurons did not show any relation between the effective observed and executed actions.

The specificity of most mirror neurons and the congruence observed in many of them between the observed and executed effective actions, renders very unlikely that their activation during gesture observation was due to monkey-experimenter interactions related to unspecific factors such as food expectancy, motor preparation for food retrieval or reward. In order, however, to control for these possibilities, we tested a group of mirror neurons

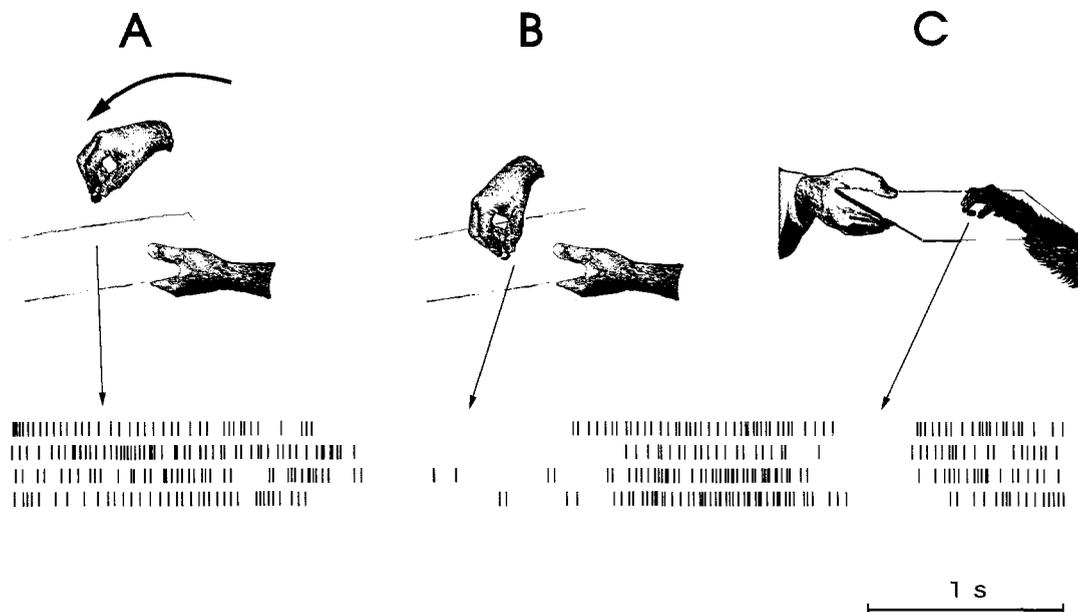


Fig. 4. Example of another highly congruent mirror neuron. A, the experimenter places a raisin on a tray. B, the experimenter grasps the same raisin. C, the monkey grasps the raisin. A response inhibition of the spontaneous discharge is present during active grasping and grasping observation. The two responses are indicated by the second and the third arrow. No changes in the spontaneous activity is present when the monkey observes the experimenter placing the food on the tray (first arrow). Four continuous recordings are shown.

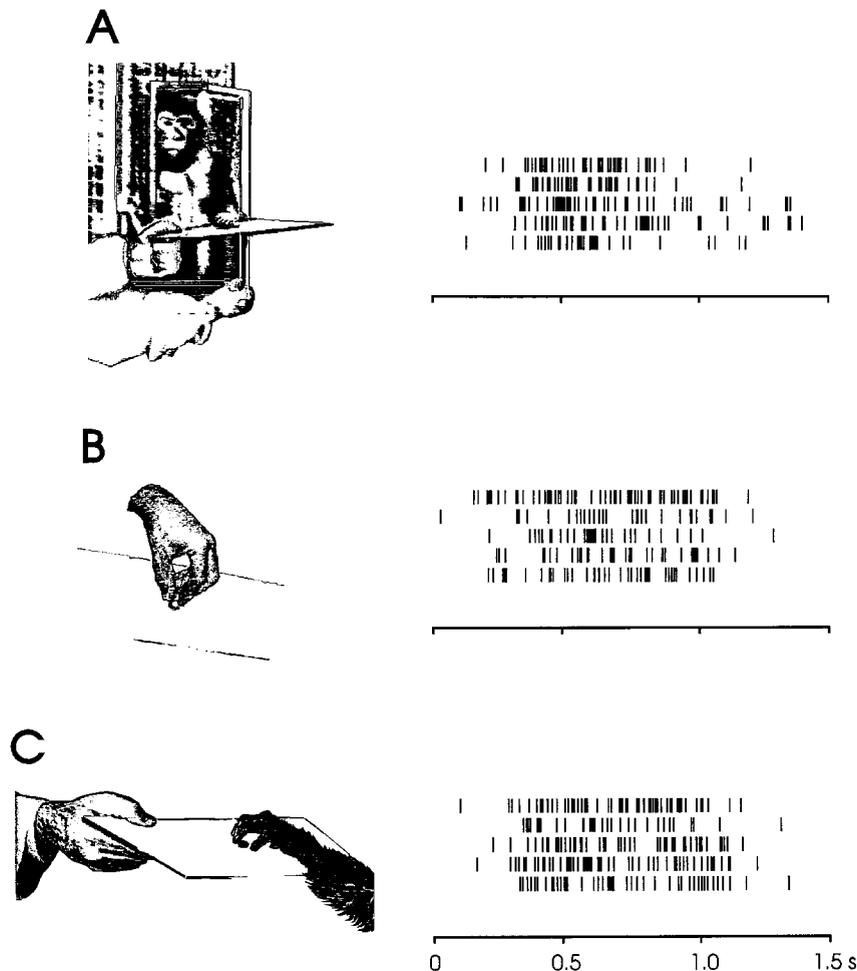


Fig. 5. Activation of a mirror neuron during the observation of grasping movements performed by a monkey seated in front of the recorded monkey (A), by the experimenter (B) and during the execution of grasping performed by the recorded monkey (C). Each panel illustrates five records of 1.5 s. The spontaneous activity was virtually absent. The neuron discharge was triggered either by the observation or execution of grasping movements.

using a second monkey as a performer of the actions. During this testing the recorded monkey had his hands restrained and did not receive food.

One of these experiments is illustrated in Fig. 5. The neuron was activated both when the recorded monkey observed grasping movements made by the second monkey (Fig. 5A) or made by the experimenter (Fig. 5B). There was also a strong response associated with grasping movements executed by the recorded monkey (Fig. 5C).

4. Discussion

4.1. Neurophysiological findings

Neurons that are selectively activated by complex biologically meaningful visual stimuli have been observed in many high-order cortical areas [5,8,18,41,44,45,49] and in the amygdala [4,26]. These neurons respond to the sight of hands, faces and particular types of body movements. Among them there are neurons, located in the depth of the

superior temporal sulcus, that are specifically responsive to hand–object interactions [44,46].

Mirror neurons of area F5 share with these ‘complex’ neurons the property of being responsive to meaningful stimuli. They differ, however, from these neurons in that they discharge also during movements performed by the observer that mimic the actions whose observation activate them. Neurons with mirror properties have been described up to now only in F5. It is likely, however, that they are not unique to this area, but do exist in other frontal and parietal cortical areas that control the organization of goal directed movements.

What may the functional role of mirror neurons be? Do they exist also in man? And if this is so, where can they be located? In the following discussion we will try to answer these questions.

4.2. Possible functional role of mirror neurons

An explanation of mirror neurons that comes naturally to mind is that they are related to motor preparation. When

the monkey observes an action, he starts automatically to prepare the same action. In this way he becomes able to perform it fast, thus prevailing on possible competitors. If this explanation is accepted, mirror neurons would be nothing else but a particular type of ‘set-related neurons’ (see [59,60]). These are a rather common type of premotor neurons that start to fire in advance of movement execution, when its target is prespecified. The ‘preparation’ explanation is unsatisfactory for two reasons. First, the discharge of mirror neurons caused by the observation of a movement is not followed by the movement that, supposedly, was prepared. The monkey looking at another monkey that grasps food does not move subsequently his fingers. Secondly, and most importantly, mirror neurons cease firing when the food is moved toward the animal and becomes available to him. If the firing of mirror neurons were related to motor preparation, the neuron activity should have increased and not decreased in the phase that precedes movement execution.

A more sophisticated interpretation of mirror neurons was given by Jeannerod [21]. In a recent review article on motor imagery he made the example of a pupil learning how to play a musical instrument. The pupil is completely still, watching the teacher who demonstrates an action that he must imitate and reproduce later. Although the pupil is immobile, he must form an image in his brain of the teacher’s action. Jeannerod’s view is that the neurons responsible for the motor image formation are the same the pupil will later activate during planning and preparation of the action. According to him mirror neurons are neurons that internally ‘represent’ an action.

The explanation we favor is similar to that proposed by Jeannerod. We also think that mirror neurons are neurons that ‘represent’ internally actions. However, whereas the emphasis given by Jeannerod is on learning, our view is that mirror neurons play a role in the understanding of motor events [9].

By the term ‘understanding motor events’ we do not imply self-consciousness (see [51]). With this term we indicate only the capacity of an individual to recognize the presence of another individual performing an action, to differentiate the observed action from other actions, and to use this information in order to act appropriately. Some of the mechanisms mediating operations of this type are linked to emotion and depend on the integrity of limbic structures (see [3]). Lesions of the amygdala, orbital frontal cortex, temporal pole produce alteration of social behavior caused, in large part, by an incapacity to produce correct response to social stimuli [50]. In contrast to the ‘understanding’ based on the affective valence of the stimuli, the ‘understanding’ mediated by mirror neurons appears to be disjoint from emotional and vegetative responses. The meaning of the observed action does not result from the emotions it evokes, but from a matching of the observed action with the motor activity which occurs when the individual performs the same action.

Biological movement implies, by definition, a change in the relations of the acting individual with the external world. These changes are signalled by proprioception, vision, and in the case of transitive actions, by touch. The consequences, positive or negative, of the movements are also monitored by senses and remembered. When an individual emits a movement, he, usually, predicts its consequences. The movement representation in the cortical areas and the movement consequences are associated. In other words the movement has a meaning (e.g. ‘grasp’) and this meaning is represented by a specific cortical activation pattern. Mirror neurons show that this movement knowledge can be attributed to actions made by others. When an external stimulus evokes a neural activity similar to that which, when internally generated, represents a certain action, the meaning of the observed action is recognized because of the similarity between the two representations, the one internally generated during action and that evoked by the stimulus. It will be too long to speculate here how the individual recognizes his own movements from those generated by others or how the pictorial aspect of the hand, which does not belong to the acting individual, becomes associated with his movement. It is enough here to say that both these problems are not impossible to solve, theoretically. What is important to stress here is that the proposed mechanism is based on a purely observation/execution matching system. The affective valence of the stimuli, even if possibly present, does not play a role in this ‘understanding’ system. We will see in the next sections the importance of this point for understanding the development of the observation/execution matching system in man.

4.3. *Observation / execution matching system in man*

The presence of an observation/execution mechanism in monkey’s premotor cortex suggests that a similar mechanism may exist also in man. To test this prediction we studied the excitability of the motor cortex in a group of normal human subjects [13]. The assumption underlying the experiment was that, if the observation of a movement activates the premotor cortex also in man, this activation should induce an enhancement of motor evoked potentials elicited by the magnetic stimulation of the motor cortex. The subjects were stimulated in four conditions: while they observed an experimenter grasping 3D-objects, while they looked at the same 3D-objects, while they observed an experimenter tracing geometrical figures in the air with his arm, and during detection of the dimming of a light. Motor evoked potentials were recorded from arm muscles.

The results showed a significant increase of the motor evoked potentials in the two conditions in which subjects observed movements. Furthermore, the increase was found only in those muscles that were active when the subjects executed the previously observed actions. Although it is premature to draw any firm conclusion on this last point,

because only two types of movements were tested, nevertheless the obtained data strongly suggest that in man there is an observation/execution matching system similar to that found in the monkey premotor cortex.

Admitted that an observation/execution matching system exists in man, the next problem is to assess where it is located. A way to discover it is to examine in which brain structures regional blood flow (rCBF) changes occur during hand movement observation.

We recently addressed this problem using positron emission tomography [53]. The experiment was carried out at the Milan PET center (ISHSR). We used three experimental conditions: Object observation, Grasping observation and Object prehension. Object observation was used as a control condition. Images were analyzed by using statistical parametric mapping (SPM).

The most striking result of the experiment was the presence, in Grasping observation condition, of a highly significant activation in the posterior part of the left inferior frontal gyrus. This region corresponds to the rostral part of Broca's area as defined by Penfield and Roberts [43]. Other active regions were present in the occipital lobe and in the middle temporal gyrus. Although not significant with the SPM procedure, a comparison between Grasping observation and Object prehension showed an activation also of the cortex in the precentral gyrus. This activation might explain the findings obtained with magnetic stimulation.

Results, at least at first glance, in contrast with ours were obtained by Decety et al. [7] in an experiment in which they studied the rCBF changes in three conditions: Object inspection, Movement observation and Motor imagery. In all three conditions the subjects were presented with 3D-objects generated by a virtual reality system. The same system generated also the image of the hand grasping the objects in Movement observation condition. The results showed an activation of the premotor areas during motor imagery, but neither premotor nor frontal activation during movement observation. In this condition the activation concerned mostly the extrastriate visual areas.

The negative results obtained by Decety et al. are not completely surprising. The virtual reality technology, as used in their experiment, is unable to create a hand identical to a human hand, but only a schematic 'hand'. Since non-biological stimuli are ineffective in exciting F5 mirror neurons (see Fig. 2), it is likely that in their experiment the cortical matching system was not activated. The moving object activated essentially visual areas and especially those involved in movement detection.

4.4. F5 and Broca's area. What is in common?

Homologies between cortical areas of different species are always difficult. They are even more difficult when one deals with speech areas, which might be unique to humans. In man, the frontal region related to speech

(Broca's area), as outlined by electrical stimulation studies [40,43], is formed by areas 44 and 45 of Brodmann. Area 44 corresponds to area FCBm of von Economo [12], while area 45 corresponds to area FD γ . The first has basically an agranular structure, while in the second a granular layer is present. Von Bonin compared the premotor cortex of human, chimpanzee and macaque monkey brains [2]. This author adopted the lettering of Von Economo and recognized an area similar in architecture to FCBm in both the chimpanzees and monkeys. In the macaque monkey the location of FCBm is basically co-extensive with the area named F5 by Matelli et al. [33]. A similarity between human and monkey's FCBm was found also by Galaburda and Pandya [15] and, more recently by Petrides and Pandya [48]. They restricted however the homology only to that part of F5 that is located in the posterior bank of the arcuate sulcus. Finally, on the basis of hodological considerations Mesulam suggested that the ventral parts of inferior area 6 (F5) and area 45 are the areas which might be the homologue of the human frontal speech areas [36].

Taken together, all these data point to F5 as the area which might be the anatomical homologue of human Broca's area. Two major differences, however, come immediately to mind. First, in F5 there is a large hand area representation, while Broca's area is classically thought of as an area related to the control of musculature responsible for spoken word production. Second, F5 is an area receiving visual and somatosensory inputs, while Broca's area is mostly related to auditory input.

Although differences in somatotopic organization between F5 and Broca's area certainly exist, these differences are probably more in terms of the extension of the somatotopic fields and detailed representation of some movements, than in terms of gross somatotopy. In F5, in addition to the hand field there is also a large mouth-face field located laterally to the former [52]. It is very likely that in man this field has grown in relations to speech development and the great motor difficulties that speech poses. The fact remains, however, that a mouth field pre-exists speech in F5. Conversely, a hand field appears to exist in the Broca's region. If clinical evidence in this sense may be questioned because of the proximity of Broca's area to motor centers controlling arm movements, some recent PET data by Petrides and collaborators suggest that this is the case [1]. These authors recently showed that during execution of a sequence of self-ordered hand movements there was a highly significant activation of Broca's area. These data fit well with the findings, reported above, that a sector of Broca's area becomes active during grasping observation.

At this point the fundamental question is the following. Is there something in common between the 'mirror' functions present in both F5 and Broca's area and Broca's speech functions? In order to answer this question, let us briefly examine what might be the possible precursors of language in monkeys.

Vocalization in response to particular stimuli is common in non-human primates. It is usually maintained, however, that speech of man and monkey vocal responses are different phenomena. First of all the structures responsible for vocal calls and speech are different. The first are mediated primarily by the cingulate cortex together with diencephalic and brain stem structure [23,29]. The second depends essentially upon the activity of a circuit, formed by the classical Wernicke and Broca's areas, which are located on the dorsolateral cortical convexity. Secondly, the monkey vocalization is intimately related to emotional and instinctive behavior, whereas speech is not. Thirdly, speech is basically a one-on-one social interaction, while vocal calls of monkeys are not aimed to one specific individual [30].

These facts led many authors to conclude that speech depends on a uniquely human neural mechanism which evolved 'de novo' [25,39,56]. This statement appears to be undeniable if vocal calls and the structures underlying them are considered the precursors of speech. There is, however, another fascinating possibility recently proposed by Mc Neillage [30]. The main tenet of McNeillage's theory is that speech evolved when a 'continual mouth open-close alternation, the two phases of which are subject to continual articulatory modulation, was superimposed on the basic mammalian mode of sound generation – larynx based phonation. The open–close alternation relates to the syllable and the open and closed phases correspond to consonants and vowel, respectively. According to the theory the vocal communication, based on open–close mandibular alternation, evolved from other mandibular cyclicities such as for example the 'lipsmacks'. This faciovisual communicative gesture occurs in a wide variety of social circumstances, it is produced by both males and females and, most importantly, is accompanied by eye contact. Thus, in contrast with vocal calls, it shows the one-on-one social interactions that characterize speech.

Summing up, according to Mc Neillage's theory, speech had its origin not in primate vocal calls, but in the primate use of communicative gestures. The communicative modality for these gestures was initially visual. Only later in evolution the communicative gestures became associated with sounds. This fundamental step led to an enormous enrichment of primate communicative possibilities which, ultimately, culminated in the appearance of speech.

The data discussed in the present article fit well with the theory of McNeillage. In addition, they offer a more general explanation of why the communication system in primates developed in the dorsolateral cortex. These data show that inferior premotor cortex is endowed with the capacity of matching an observed action with an executed action and that, very likely, this mechanism is at the basis of monkey understanding of actions made by other individuals. If this conclusion is correct, the functional specialization of human Broca's area derives from an ancient mechanism related to production and understanding of motor

acts. From this mechanism evolved, possibly in relation with the development of a more complex social life, first the capacity to make and interpret facial communicative gestures and, then, the capacity to emit and understand 'verbal gestures'. It is likely that the sophisticated capacity of movement analysis shown by mirror cells is at the basis of the evolutionary prevalence of the lateral motor system on the medial one, related to emotion, in becoming the main communication channel in higher primates and man.

Acknowledgements

The work was supported by the Human Frontier Science Program and by grants from CNR and MURST to G.R.

References

- [1] Bonda, E., Petrides, M., Frey, S. and Evans, A.C., Frontal cortex involvement in organized sequences of hand movements: evidence from a positron emission tomography study, *Soc. Neurosci. Abstr.*, (1994) 152.6.
- [2] von Bonin, G., Architecture of the precentral motor cortex and some adjacent areas. In P. Bucy (Ed.), *The Precentral Motor Cortex*, University of Illinois Press, Urbana, 1944, pp. 7–82.
- [3] Brothers, L., The social brain: a project for integrating primate behavior and neurophysiology in a new domain, *Concepts Neurosci.*, 1 (1990) 27–51.
- [4] Brothers, L., Ring, B. and Kling, A., Response of neurons in the macaque amygdala to complex social stimuli, *Behav. Brain Res.*, 41 (1990) 199–213.
- [5] Bruce, C., Desimone, R. and Gross, C.G., Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque, *J. Neurophysiol.*, 46 (1981) 369–384.
- [6] Cavada, C. and Goldman-Rakic, P.S., Posterior parietal cortex in rhesus monkey. II. Evidence for segregated corticocortical networks linking sensory and limbic areas with the frontal lobe, *J. Comp. Neurol.*, 287 (1989) 422–445.
- [7] Decety, J., Perani, D., Jeannerod, M., Bettinardi, V., Tadary, B., Woods, R., Mazziotta, J.C. and Fazio, F., Mapping motor representations with positron emission tomography, *Nature*, 371 (1994) 600–602.
- [8] Desimone, R., Albright, T.D., Gross, C.G. and Bruce, C., Stimulus-selective properties of inferior temporal neurons in the macaque, *J. Neurosci.*, 8 (1984) 2051–2062.
- [9] di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V. and Rizzolatti, G., Understanding motor events: a neurophysiological study, *Exp. Brain Res.*, 91 (1992) 176–180.
- [10] Dum, R.P. and Strick, P.L., The origin of corticospinal projections from the premotor areas in the frontal lobe, *J. Neurosci.*, 11 (1991) 667–689.
- [11] Dum, R.P. and Strick, P.L., Premotor areas: nodal points for parallel efferent systems involved in the central control of movement. In D.R. Humphrey and H.-J. Freund (Eds.), *Motor Control: Concepts and Issues. Dahlem workshop reports*, Wiley, Chichester, 1991, pp. 383–397.
- [12] von Economo, C., *The Cytoarchitectonics of the Human Cerebral Cortex*, Oxford University Press, London, 1929.
- [13] Fadiga, L., Fogassi, L., Pavesi, G. and Rizzolatti, G., Motor facilitation during action observation: a magnetic stimulation study, *J. Neurophysiol.*, 73 (1995) 2608–2611.

- [14] Ferrigno, G. and Pedotti, A., ELITE: a digital dedicated hardware system for movement analysis via real-time TV-signal processing, *IEEE Trans. Biomed. Eng.*, BME-32, 11 (1985) 943–950.
- [15] Galaburda, A.M. and Pandya, D.N., Role of architectonics and connections in the study of primate brain evolution. In E. Armstrong and D. Falk (Eds.), *Primate Brain Evolution*, Plenum, New York, 1982, pp. 203–216.
- [16] Gallese, V., Murata, A., Kaseda, M., Niki, N. and Sakata, H., Deficit of hand reshaping after muscimol injection in monkey parietal cortex, *NeuroReport*, 5 (1994) 1525–1529.
- [17] Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M., Camarda, R. and Rizzolatti, G., Functional organization of inferior area 6 in the macaque monkey. I. Somatotopy and the control of proximal movements, *Exp. Brain Res.*, 71 (1988) 475–490.
- [18] Gross, C.G., Rocha-Miranda, C.E. and Bender, D.E., Visual properties of neurons in the inferotemporal cortex of the macaque, *J. Neurophysiol.*, 35 (1972) 96–111.
- [19] He, S.Q., Dum, R.P. and Strick, P.L., Topographic organization of corticospinal projections from the frontal lobe – motor areas on the lateral surface of the hemisphere, *J. Neurosci.*, 13 (1993) 952–980.
- [20] Hepp-Reymond, M.-C., Hübler, E.J., Maier, M.A. and Qi, H.-X., Force-related activity in two regions of the primate ventral premotor cortex, *Can. J. Physiol. Pharmacol.*, 72 (1994) 571–579.
- [21] Jeannerod, M., The representing brain: neural correlates of motor intention and imagery, *Behav. Brain Sci.*, 17 (1994) 187–245.
- [22] Jeannerod, M., Arbib, M.A., Rizzolatti, G. and Sakata, H., Grasping objects: the cortical mechanisms of visuomotor transformation, *Trends Neurosci.*, 18 (1995) 314–320.
- [23] Jurgens, U., Primate communication: signalling, vocalization. In G. Adelman (Ed.), *Encyclopedia of Neuroscience*, Birkhauser, Boston, 1987.
- [24] Kurata, K. and Tanji, J., Premotor cortex neurons in macaques: activity before distal and proximal forelimb movements, *J. Neurosci.*, 6 (1986) 403–411.
- [25] Lancaster, J., *Primate behavior and the emergence of human culture*, Holt, Rinehart Winston, New York, 1973.
- [26] Leonard, C.M., Rolls, E.T., Wilson, F.A.W. and Baylis, G.C., Neurons in the amygdala of the monkey with responses selective for faces, *Behav. Brain Res.*, 15 (1985) 159–176.
- [27] Luppino, G., Matelli, M., Camarda, R., Gallese, V. and Rizzolatti, G., Multiple representations of body movements in mesial area 6 and the adjacent cingulate cortex: an intracortical microstimulation study, *J. Comp. Neurol.*, 311 (1991) 463–482.
- [28] Luppino, G., Matelli, M. and Rizzolatti, G., Cortico-cortical connections of two electrophysiologically identified arm representations in the mesial agranular frontal cortex, *Exp. Brain Res.*, 82 (1990) 214–218.
- [29] MacLean, P.D., Introduction: perspectives on cingulate cortex in the limbic system. In B.A. Vogt and M. Gabriel (Eds.), *Neurobiology of Cingulate Cortex and Limbic Thalamus: a Comprehensive Handbook*, Birkhauser, Boston, 1993.
- [30] MacNeilage, P.F., The frame/content theory of evolution of speech production, *Behav. Brain Sci.*, in press.
- [31] Matelli, M., Camarda, R., Glickstein, M. and Rizzolatti, G., Afferent and efferent projections of the inferior area 6 in the macaque monkey, *J. Comp. Neurol.*, 251 (1986) 281–298.
- [32] Matelli, M., Luppino, G., Murata, M. and Sakata, H., Independent anatomical circuits for reaching and grasping linking the inferior parietal sulcus and inferior area 6 in macaque monkey, *Soc. Neurosci. Abstr.*, 20 (1994) 404.4.
- [33] Matelli, M., Luppino, G. and Rizzolatti, G., Patterns of cytochrome oxidase activity in the frontal agranular cortex of macaque monkey, *Behav. Brain Res.*, 18 (1985) 125–137.
- [34] Matelli, M., Luppino, G. and Rizzolatti, G., Architecture of superior and mesial area 6 and of the adjacent cingulate cortex, *J. Comp. Neurol.*, 311 (1991) 445–462.
- [35] Matsumura, M. and Kubota, K., Cortical projection of hand–arm motor area from postarcuate area in macaque monkey: a histological study of retrograde transport of horseradish peroxidase, *Neurosci. Lett.*, 11 (1979) 241–246.
- [36] Mesulam, M.M., Large-scale neurocognitive networks and distributed processing for attention, language, and memory, *Ann. Neurol.*, 28 (1990) 597–613.
- [37] Muakkassa, K.F. and Strick, P.L., Frontal lobe inputs to primate motor cortex: evidence for four somatotopically organized 'premotor' areas, *Brain Res.*, 177 (1979) 176–182.
- [38] Mushiaki, H., Inase, M. and Tanji, J., Neuronal activity in the primate premotor, supplementary, and precentral motor cortex during visually guided and internally determined sequential movements, *J. Neurophysiol.*, 66 (1991) 705–718.
- [39] Myers, R.E., Comparative neurology of vocalization and speech: proof of a dichotomy, *Ann. New York Acad. Sci.*, 280 (1976) 745–757.
- [40] Ojemann, G.A., Brain organization for language from the perspective of electrical stimulation mapping, *Behav. Brain Sci.*, 2 (1983) 189–230.
- [41] Oram, M.W. and Perrett, D.I., Responses of anterior superior temporal polysensory (STPa) neurons to 'biological motion' stimuli, *J. Cogn. Neurosci.*, 6 (1994) 99–116.
- [42] Passingham, R., *The Frontal Lobes and Voluntary Action*, Oxford, Oxford University Press, 1993, pp. 299.
- [43] Penfield, W. and Roberts, L., *Speech and Brain Mechanisms*, Princeton University Press, Princeton, 1959.
- [44] Perrett, D.I., Harries, M.H., Bevan, R., Thomas, S., Benson, P.J., Mistlin, A.J., Chitty, A.K., Hietanen, J.K. and Ortega, J.E., Frameworks of analysis for the neural representation of animate objects and actions, *J. Exp. Biol.*, 146 (1989) 87–113.
- [45] Perrett, D.I., Rolls, E.T. and Caan, W., Visual neurones responsive to faces in the monkey temporal cortex, *Exp. Brain Res.*, 47 (1982) 329–342.
- [46] Perrett, D.I., Mistlin, A.J., Harries, M.H. and Chitty, A.J., Understanding the visual appearance and consequence of hand actions. In M.A. Goodale (Ed.), *Vision and Action: the Control of Grasping*, Ablex, Norwood, NJ, 1990, pp. 163–180.
- [47] Petrides, M. and Pandya, D.N., Projections to the frontal cortex from the posterior parietal region in the rhesus monkey, *J. Comp. Neurol.*, 228 (1984) 105–116.
- [48] Petrides, M. and Pandya, D.N., Comparative architectonic analysis of the human and the macaque frontal cortex. In F. Boller and J. Grafman (Eds.), *Handbook of Neuropsychology*, Vol. IX, Elsevier, New York, 1994, pp. 17–58.
- [49] Pigarev, I.N., Rizzolatti, G. and Scandolara, C., Neurons responding to visual stimuli in the frontal lobe of macaque monkeys, *Neurosci. Lett.*, 12 (1979) 207–212.
- [50] Price, J.L., Russchen, F.T. and Amaral, D.G., The amygdaloid complex. In L.W. Swanson, A. Björklund and T. Hökfelt (Eds.), *Handbook of Chemical Neuroanatomy*, Elsevier, New York, 1987, pp. 279–388.
- [51] Rizzolatti, G., Nonconscious motor images, *Behav. Brain Sci.*, 17 (1994) 220.
- [52] Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G. and Matelli, M., Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements, *Exp. Brain Res.*, 71 (1988) 491–507.
- [53] Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Perani, D. and Fazio, F., Localization of cortical areas responsive to the observation of hand grasping movements in humans: a PET study, submitted.
- [54] Rizzolatti, G., Gentilucci, M., Camarda, R., Gallese, V., Luppino, L., Matelli, M. and Fogassi, L., Neurons related to reaching-grasping arm movements in the rostral part of area 6 (area 6a β), *Exp. Brain Res.*, 82 (1990) 337–350.
- [55] Rizzolatti, G., Scandolara, C., Gentilucci, M. and Camarda, R.,

- Response properties and behavioural modulation of 'mouth' neurons of the postarcuate cortex (area 6) in macaque monkey, *Brain Res.*, 255 (1981) 421–424.
- [56] Robinson, B.W., Limbic influences on human speech, *Ann. New York Acad. Sci.*, 280 (1976) 761–771.
- [57] Sakata, H., Taira, M., Mine, S. and Murata, A., Hand-movement related neurons of the posterior parietal cortex of the monkey: their role in visual guidance of hand movements. In R. Caminiti, P.B. Johnson and Y. Burnod (Eds.), *Control of Arm Movement in Space*, *Exp. Brain Res., Suppl. 22*, Springer-Verlag, Berlin, 1992, pp. 185–198.
- [58] Taira, M., Mine, S., Georgopoulos, A.P., Murata, A. and Sakata, H., Parietal cortex neurons of the monkey related to the visual guidance of hand movement, *Exp. Brain Res.*, 83 (1990) 29–36.
- [59] Weinrich, M., Wise, S.P. and Mauritz, K.M., A neurophysiological study of the premotor cortex in the rhesus monkey, *Brain*, 107 (1984) 385–414.
- [60] Wise, S.P., The primate premotor cortex: past, present and preparatory, *Annu. Rev. Neurosci.*, 8 (1985) 1–19.