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3

Cortical Mechanisms Subserving Object Grasping and Action Recognition: A New View on the Cortical Motor Functions

GIACOMO RIZZOLATTI, LEONARDO FOGASSI, AND VITTORIO GALLESE

ABSTRACT This chapter provides evidence for a new and broader view of the functions of the cortical motor system. On the basis of the functional properties of a monkey premotor area (area F5), the authors propose that at the core of the cortical motor systems there are vocabularies of motor actions. Neurons forming these vocabularies store knowledge about actions and the description of how this knowledge must be applied. When a specific population of these neurons becomes active, an internal copy of a specific action is generated. This copy may be used for two purposes: (1) planning and executing goal-directed actions or (2) recognizing actions made by another individual. The action recognition is based on a match between an observed action and its internal motor copy. Finally, evidence is reviewed showing that an action observation/execution matching system, similar to that of the monkey, also is present in humans.

"The motor systems of the brain exist to translate thought, sensation and emotion into movement. At present the initial steps of this process lie beyond analysis. We do not know how voluntary movements are engendered, nor where the 'orders' come from" (Henneman, 1984). This sentence, which starts the section on the organization of the motor system in the classic *Medical Physiology*, edited by Mountcastle, expresses well the prevalent ideas about the motor system: The motor system deals with *movements*. The processes that lead to them are remote processes virtually inaccessible to neurophysiological inquiry.

The view proposed in this chapter is different. First, we challenge the view that *movement* is at the core of the motor system. *Action* is. Unlike movement, action is defined by a goal and by an expectancy. Movements are the final outcome of action and are programmed and controlled as such only when action is set and executed.

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Second, motor system is involved not exclusively in action generation but also plays an important role in matching the external reality on the internally produced actions. We submit that in primates, this second role is by no means secondary but has a great importance for recognizing actions made by others.

Although we believe that these concepts are valid in general for the mosaic of motor areas forming the agranular frontal cortex, in this chapter, we use as an example the organization of one monkey premotor area, area F5. In this area, the two aspects of the motor system, action generation and action recognition, clearly emerge.

Motor properties of F5 neurons

Figure 38.1 shows a lateral view of the monkey brain. Area F5 forms the rostral part of inferior area 6. It is located anterior to area F4 and extends into the posterior bank of the inferior arcuate sulcus (Matelli, Luppino, and Rizzolatti, 1985).

Area F5 is not homogeneous. At least two morphologically distinct sectors can be distinguished in it, F5 of the convexity (F5c) and F5 forming the posterior bank of the arcuate sulcus (F5ab) (Matelli et al., 1996). Corticospinal fibers originate from F5ab only (He, Dum, and Strick, 1993).

Intracortical microstimulation studies and neuron recordings showed that area F5 is involved in the control of hand and mouth movements. (Rizzolatti et al., 1981a, 1981b; Kurata and Tanji, 1986; Gentilucci et al., 1988; Rizzolatti et al., 1988; Hepp-Reymond et al., 1994). Although there is a considerable overlap between the two representations, hand movements are located more dorsally, whereas mouth movements are located more ventrally (Gentilucci et al., 1988).

Particularly important for understanding the function of F5 are the results obtained by testing F5 neurons in a



FIGURE 38.1 Lateral view of macaque monkey cerebral cortex showing frontal and parietal areas. The intraparietal sulcus is opened to show areas located in its medial and lateral banks. Frontal agranular cortical areas are classified according to Mattelli et al. (1985). The cortical areas of the parietal convexity are classified according to Von Bonin and Bailey (1947). Abbreviations: AIP, anterior intraparietal area; LIP, lateral intraparietal area; MIP, medial intraparietal area; VIP, ventral intraparietal area.

naturalistic context (Rizzolatti et al., 1988). Awake monkeys were seated on a primate chair and presented with various objects (geometric solids, pieces of food of different size and shape). The stimuli were introduced in various spatial locations around the monkey, inside and outside its peripersonal space. After object presentation, the monkey was allowed to reach and grasp the objects.

The results confirmed that most neurons become active in relation to distal movements. However, they also showed that the neuron discharge typically correlates much better with an action or with fragments of an action (motor acts) rather than with the movements forming it. Thus, many neurons discharge when an action (e.g., grasping) is performed with effectors as different as the right hand, the left hand, or the mouth. An example of this behavior is shown in figure 38.2. Furthermore, in most neurons, the same type of movement (e.g., an index finger flexion) effective in triggering a neuron during grasping made with the index finger and the thumb was not effective during grasping made using all fingers. Thus, in these cases, the characterization of neuron activity in terms of individual movements is meaningless.

By using actions as classification criteria, F5 neurons were subdivided into the following main categories: grasping-with-the-hand-and-the-mouth neurons, grasping-with-the-hand neurons, holding neurons, tearing neurons, poking neurons, and manipulating neurons. Grasping neurons were the neuron type most represented (Rizzolatti et al., 1988).

Grasping is a complex action characterized by an initial opening phase, during which fingers are shaped according to the object physical properties (size, shape) and the wrist is adapted to object orientation, and a second, closure phase, in which fingers are flexed around the object until they touch it (Jeannerod, 1988). The type of hand shape depends on the size and shape of the object to be grasped. The three grip types that monkeys most frequently use are: precision grip, which is opposition of the thumb to the index finger (used for grasping small objects); finger prehension, which is opposition of the thumb to the other fingers (used to grasp middle-sized objects or to retrieve them from a narrow container); and whole-hand (or power) prehension, which is opposition of the fingers to the palm (used to grasp large objects). Neurons were recorded while monkeys grasped objects using these three grip types.

The results showed that most (85%) grasping neurons are selective for one of the three main grip types. The most represented type is precision grip, the least represented is whole-hand prehension. There is specificity for different finger configurations even within the same general type of grip. Thus, for example, in the case of whole-hand prehension, the prehension of a sphere, which requires the opposition of all fingers, is encoded by different neurons than the prehension of a cylinder, for which a palm opposition grip, thumb excluded, is required (figure 38.3).

Both neurons selective for a specific grip type and those unspecific showed a variety of temporal relations with the prehension phases. Some F5 neurons discharged during the whole action coded by them, sometimes starting to fire at stimulus presentation. Some were active mostly during the opening of the fingers, some during finger closure (Jeannerod et al., 1995).

A METHODOLOGICAL INTERLUDE Before discussing the theoretical importance of these findings, a methodological point must be stressed. Typically, in neuron studies of the motor cortex, the behavioral or ethological context in which movements are emitted are considered of little or no importance. The variable that is controlled is movement. Paradigmatic in this sense are the experiments of Evars, in which the animal had simply to move the wrist or exert a force (Evars, 1981).

Had this approach been used in the study of F5, the most important characteristics of its neurons would have been lost. For example, it would have been impossible to discover that that same neuron discharges during mouth grasping and hand grasping. Similarly, because many grasping neurons produce a weak response during an inappropriate movement (e.g., a finger flexion), their

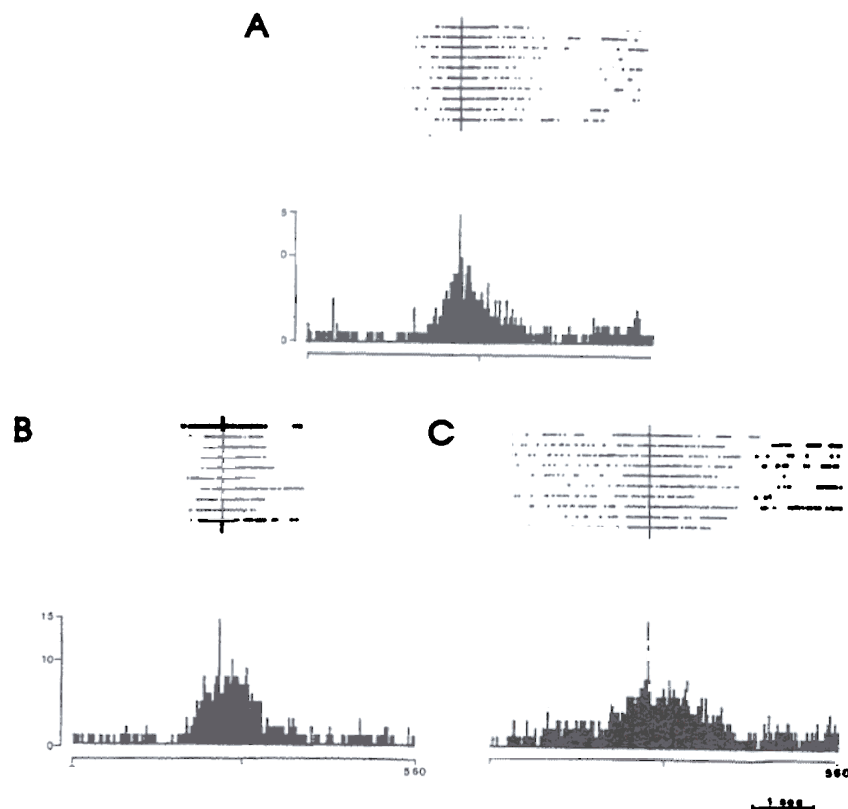


FIGURE 38.2 Example of a "grasping-with-the-hand-and-the-mouth" F5 neuron. (A) Neuron discharge during grasping with the mouth. (B) Neuron discharge during grasping with the hand contralateral to the recorded hemisphere. (C) Neuron discharge during grasping with the hand ipsilateral to the re-

corded hemisphere. Rasters and histograms are aligned with the moment in which the monkey touched the food. The histograms are the sum of ten trials. Abscissae: time expressed in bins. Bin width: 10 ms. Ordinate: spikes/bin. (Modified from Rizzolatti et al., 1988.)

main characteristic (e.g., that of firing during specific motor action) also would have passed unnoticed.

The results of F5 study indicate that for cortical motor neurons, the same strategy should be used as that so successfully adopted in the sensory systems. For each neuron, the specific motor triggering feature must be established, and for those responding to passive stimuli, the sensory triggering features also must be assessed. Only, at this point, specific behavioral tasks can be adopted. Without such a strategy, one would never

"know how voluntary movements are engendered, nor where the 'orders' come from."

A "VOCABULARY" OF MOTOR ACTION Some years ago, Arbib (1981) proposed to describe the behavior of individuals in terms of schemas. A schema is both a store of knowledge and the description of a process for applying that knowledge. The schema idea can be applied at the single neuron level. The properties of F5 neurons fit this definition. These neurons store specific

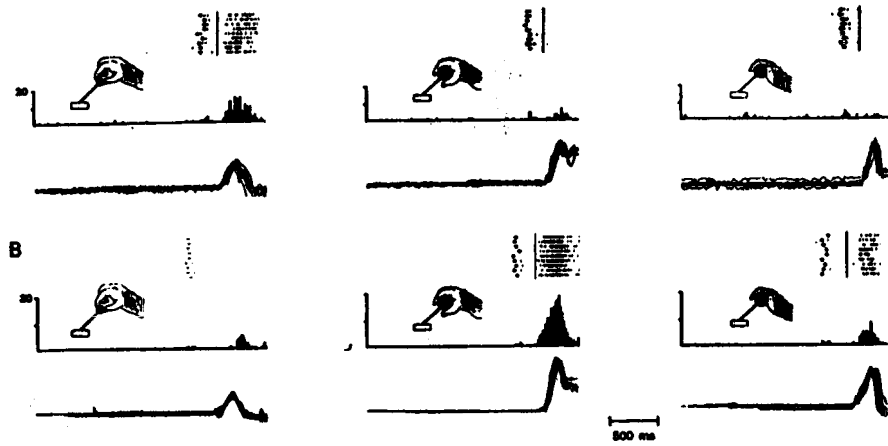


FIGURE 38.3 Examples of two F5 "grasping-with-the-hand" purely motor neurons. Recordings were made during the following behavioral task; the monkey was seated in front of a dark box. Trials began when the monkey pressed a keypad. Pressing the keypad illuminated the box, and a geometric solid located inside of it became visible. After a variable delay, the front door of the box opened, allowing the monkey to reach for and grasp the object. (A) Neuron selective for precision grip. (B) Neuron selective for whole-hand prehension. Rasters

and histograms and the distance between the thumb and the index finger (recorded with a computerized movement analyzer) are shown, aligned with the onset of hand movement (vertical bar). Dots indicate the opening of the box front door. The grasped objects were, from left to right: a small sphere, a large sphere, and a horizontally oriented cylinder. Abscissae: time expressed in ms; ordinates: spikes/bin. Bin width: 20 ms. (Modified from Jeannerod et al., 1995.)

knowledge about an action and, when activated, indicate how to implement it.

F5 is a store of motor schemas or, using the terminology of Rizzolatti (Rizzolatti and Gentilucci, 1988; Gentilucci and Rizzolatti, 1990) a "vocabulary" of actions. This motor vocabulary is constituted by "words," each of which is represented by a set of F5 neurons. Some words indicate the general goal of an action (e.g., grasping, holding, tearing); others indicate the way in which a specific action must be executed (e.g., precision grip or finger prehension). Finally, other words are concerned with the temporal segmentation of the action into motor acts, each coding a specific phase of the grip (e.g., hand opening, hand closure).

The view that F5 contains a vocabulary of motor schemas has important functional implications. First, the presence of such a vocabulary strongly facilitates the execution of motor commands. The existence of neurons, which represent specific motor schemas and are anatomically linked (hard-wired) with cortical (F1) and subcortical motor centers, facilitates the selection of the most appropriate combination of movements by reducing the number of variables that the motor system has to control to achieve the action goal. Second, it simplifies

the association between a given stimulus (i.e., a visually presented object) and the appropriate motor response toward it. Third, it gives the brain a storage of motor schemas (i.e., a knowledge about actions) that, as we show in the next sections, provides the motor system with functions traditionally attributed to the sensory systems.

Canonical F5 neurons

The motor properties of F5 we described in the previous section are proper to all F5 neurons. Studies of the responsiveness of F5 neurons have shown that many of them respond to visual stimuli. According to the type of effective visual stimulus, the responsive neurons (visuomotor neurons) were subdivided into two main categories. Neurons of the first category discharge when the monkey observes graspable objects. As evident in a forthcoming section, these neurons play a role in object-to-hand movement transformations. Because visuomotor transformation is a function traditionally attributed to the ventral premotor cortex, we refer to them as "canonical" F5 neurons. Neurons of the second category discharge when the monkey observes another individual making an

action in front of it. We refer to these neurons as "mirror neurons" (Gallese et al., 1996; Rizzolatti et al., 1996a).

The two categories of F5 neurons are located in two different subregions of area F5: canonical neurons are found mainly in F5ab, whereas mirror neurons are recorded almost exclusively from the cortical convexity (F5c).

VISUAL PROPERTIES OF CANONICAL F5 NEURONS Experiments in which F5 neurons were tested using natural stimuli showed that many F5 neurons became active in response to object presentation (Rizzolatti et al., 1988). Recently (Murata et al., 1997), the visual responses of F5 neurons to object presentation were re-examined using a formal behavioral paradigm originally devised by Sakata (Murata et al., 1996). The paradigm was basically as follows.

The monkey faced a dark box where geometric objects (e.g., cube, cylinder, sphere) of different size and shape were located. The objects were presented one at a time. The trial started with the presentation of a colored spot of light on the object that remained invisible. At the spot presentation, the monkey had to fixate it and press a bar. The bar pressing illuminated the box and made the object visible. After a variable delay, the spot changed color. This was the signal for the monkey to release the bar and reach and grasp the object ("grasping in light" condition). In a second condition, all the events were as aforementioned, but when the spot changed color, the monkey had only to release the bar. Object grasping was not allowed ("object fixation" condition). The two conditions were run in different blocks, and the spot colors in them were different. In a third condition ("grasping in dark" condition), the same object was presented for many consecutive trials. The monkey saw the object before the beginning of the first experimental trial, and therefore knew its characteristics, but it had to perform the entire task without visual guidance. Eye movements were controlled in all conditions.

The results showed that approximately half of the tested neurons responded to three-dimensional (3-D) object presentation and two thirds of them were selective to one specific object or to a cluster of objects. A strict congruence between visual and motor selectivity was found in most recorded neurons. Figure 38.4 shows the responses of a visually selective neuron. Observation and grasping of the ring produced strong responses (figure 38.4A). Responses to the other five objects were modest (sphere) or virtually absent.

Figures 38.4B and C show the behavior of the same neuron in two other experimental conditions: object fixation and object grasping in dark. In the object fixation condition, the objects were presented as aforementioned,

but at the go signal, instead of grasping the object, the monkey had to release a key. Grasping was not allowed. In this condition, the object is totally irrelevant for task solution, which only requires the detection of the go signal (spot color change). However, the neuron strongly discharged at the presentation of the preferred object (figure 38.4B).

The behavior of the neuron during object grasping in dark is illustrated in figure 38.4C. In the absence of any visual stimulus, the neuron discharged in association with ring grasping. The movement-related discharge was preceded by a sustained activity.

How can these findings be explained? At the onset, the object related visual responses could not be attributed to unspecific factors, such as attention or "intention" (desire to grasp the object). If either of these possibilities were true, the neuron would have not shown object specificity. Attention and "intention" are the same, regardless of which is the object presented. How can the neuron response to the object be interpreted?

Before answering this question, we must consider that a discharge extracellularly recorded from a neuron represents the output of this neuron regardless of how the neuron is excited. Thus, the responses of a given F5 neuron must be either visual, with the responses reflecting the physical aspect of the object, or motor, dealing with the activation of a motor schema—that is, the "idea" of how a motor effector must interact with the object.

The fact that F5 is a premotor area suggests that the object-related F5 neurons responses should represent objects in motor terms. Every time an object is presented, it triggers an immediate retrieval of the specific word of the motor vocabulary related to that object. Therefore, regardless of any intention to move (see "object fixation condition"), the "visual" response to object presentation would be the translation of the object into a potential motor action. The representation of this potential action then is kept active during the period following object presentation (see the sustained response following object presentation) and is transformed in overt movement only when the response is allowed.

Preliminary experiments from our laboratory confirm this interpretation (see also Murata et al., 1997). A large number of visually responsive neurons discharge to the presentation of objects that, although differing in shape (i.e., cube, cone, sphere), nevertheless are grasped in the same way.

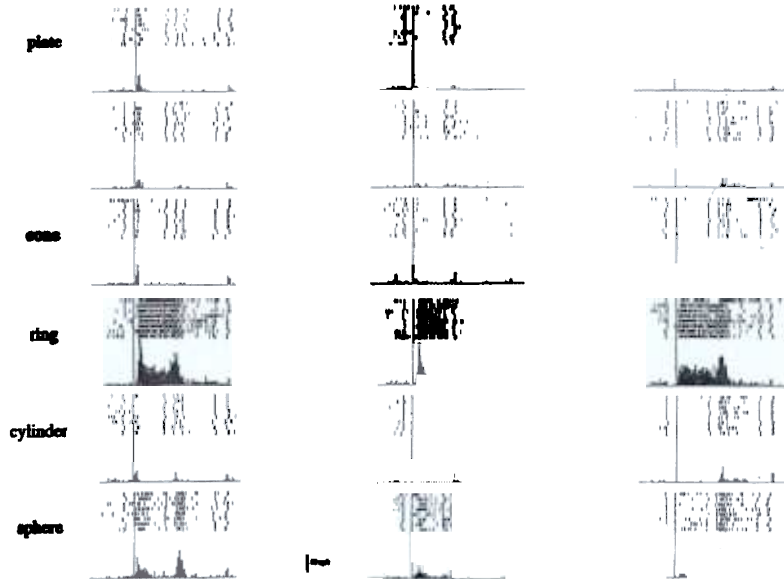
The AIP-F5 grasping circuit

VISUAL INPUT TO F5: AREA AIP Regardless of the interpretation of their discharge, there is no doubt that many F5 neurons respond to visual stimuli. Which is the

visual and motor neurons—have discharge properties similar to those of motor and visuomotor F5 neurons, respectively, whereas the third class—visual dominant neurons—is not present in F5. Visual dominant neurons are active during object fixation and grasping movements executed under visual guidance, but they do not respond when the same movements are executed in darkness (Sakata et al., 1995).

Like F5 neurons, many AIP neurons are selective for object shape and size. Among those classified as visual and motor neurons, many show the same selectivity during both object fixation and object grasping.

Although F5 and AIP share many common features, there also are some differences between them. In particular: (1) visual responses to 3-D objects are observed more frequently in AIP than in F5; (2) virtually all F5 neurons have motor properties, whereas these properties are present only in a set of AIP neu-



Control



Muscimol (site B)



FIGURE 38.5 Preshaping and actual grasping of a small plate in a groove. *Top row:* single frame images redrawn from video and stick diagram of a typical control trial. During preshaping, the monkey extends its index finger and simultaneously flexes the last three fingers. Actual grasping is achieved by opposing the thumb and the index finger (precision grip). *Bottom row:*

single frame images redrawn from video and stick diagram of a single trial performed after muscimol microinjection in area AIP. During preshaping, flexion of the last three fingers did not occur, and thumb-index finger opposition could not be executed. (Modified from Gallese et al., 1994.)

rons; (3) visual dominant neurons are present only in AIP; and (4) most AIP neurons discharge during the whole grasping action, whereas this occurs only in some F5 neurons, F5 neurons discharging more frequently only in some of the phases in which grasping is subdivided.

successful grasping, the grip very often was achieved after several correction movements that relied on tactile exploration of the object. A deficit in reaching never was observed.

INACTIVATION STUDIES The data discussed thus far strongly suggest that the AIP-F5 circuit is involved in visuomotor transformations for grasping. This role of the AIP-F5 circuit recently was proved directly by inactivation data.

Figure 38.5 illustrates the grip of a small plate positioned in a groove performed before (upper part) and after (lower part) AIP inactivation. After inactivation, hand preshaping was disrupted completely; the monkey did not flex its last three fingers and very often failed to insert the index finger into the groove. When the monkey occasionally succeeded in inserting it, it nevertheless was unable to oppose the finger to the thumb.

The effect of inactivation of AIP (muscimol injections) on grasping behavior was studied by Gallese and colleagues (1994). They trained a monkey to reach for and grasp geometric solids of different size and shape, each of which required a specific pattern of finger movements to be grasped adequately.

Preliminary experiments in which muscimol was injected into F5ab—that is, in the F5 sector in which canonical neurons are located—produced similar deficits. The impairment was limited to precision grip of the hand contralateral to the lesion when small injections were made. Larger injections produced bilateral deficit concerning all grip types (Gallese et al., 1997).

After muscimol injection, the behavior of the hand contralateral to the injection side was markedly impaired. Severe disruption of preshaping of the hand was observed constantly. As a consequence, there was a mismatch between the 3-D features of the objects to be grasped, especially of the small ones, and the posturing of finger movements, leading either to a complete failure of prehension or to an awkward grasping. In the case of

VISUOMOTOR TRANSFORMATION FOR GRASPING: A POSSIBLE NEURAL MODEL The functional properties of F5 and AIP just reviewed allow one to propose a model that can explain how the AIP-F5 circuit transforms visual information into action. Mainly, the AIP visual

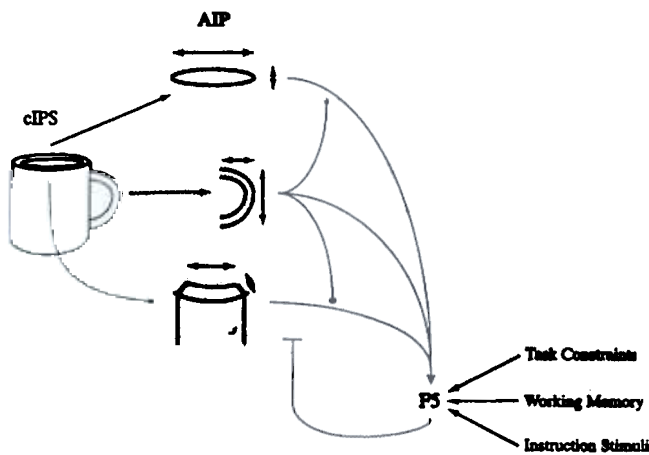


FIGURE 38.6 Cartoon schematically representing a model of AIP-F5 interactions for hand grasping under visual guidance. The figure shows an object that may be grasped in various ways. The object is analyzed by the posterior part of the inferior

parietal cortex (cIPS area) and by AIP. The selection of prehension type occurs in area F5. (Modified from Fagg and Arbib, 1998.)

dominant neurons receive information on object properties from 3-D object sensitive neurons located in an area posterior to LIP, called caudal IPS (cIPS, see Shikata et al., 1996). The AIP neurons extract from this global object description some specific aspects. For example, in the case of the mug shown in figure 38.6, AIP neurons respond to the handle of the mug, to its body, or its body upper border. Therefore, they parcellate the global object into its parts. This multiple description then is sent to F5, "proposing" various grasping possibilities. One of them is chosen. The choice depends on the concomitant information (purpose of the grasping, internal drive, spatial relationship with other objects) that F5 receives from the prefrontal lobe by means of other premotor areas or directly. On the basis of joint AIP input and visual and nonvisual contextual information, a grasping schema (e.g., precision grip) is selected. This schema then (1) is sent back to AIP by way of motor dominant neurons, allowing matching between the selected movement pattern and the visual input during action execution and (2) activates in sequence the various motor act schemas forming the grasping actions (e.g., hand opening, hand closure). These motor act schemas provide the necessary information to F1 and subcortical centers for action execution. A computational model of the AIP-F5 circuit based on principles similar to those just described recently was proposed by Fagg and Arbib (1998; Fagg, 1996).

Mirror F5 neurons

In addition to canonical neurons, in F5, there is a second category of visuomotor neurons. These neurons become active both when the monkey performs an action and when it observes a similar action made by another monkey or by the experimenter. The presentation of 3-D objects, even when held by the hand, does not evoke the neuron discharge. These neurons have been named "mirror neurons" (Gallese et al., 1996; Rizzolatti et al., 1996a). An example is shown in figure 38.7.

To discover the trigger features of mirror neurons, Rizzolatti and coworkers (1996a; Gallese et al., 1996) presented the monkey with a series of actions. They were transitive actions (such as grasping, holding, manipulating, or tearing objects), intransitive movements with emotional content (e.g., threatening gestures) or without it (e.g., arms lifting). Furthermore, to control whether a recorded neuron responded specifically to hand-objects interactions, the following actions also were performed: hand movements mimicking object-related actions in the absence of the objects; prehension movements made using tools such as pincers or pliers; simultaneous movements of hands and objects kept spatially separated. Finally, to rule out the possibility that mirror neurons activation could be due to unspecific factors such as food expectancy or motor preparation for food retrieval or reward, a group of neurons were stud-

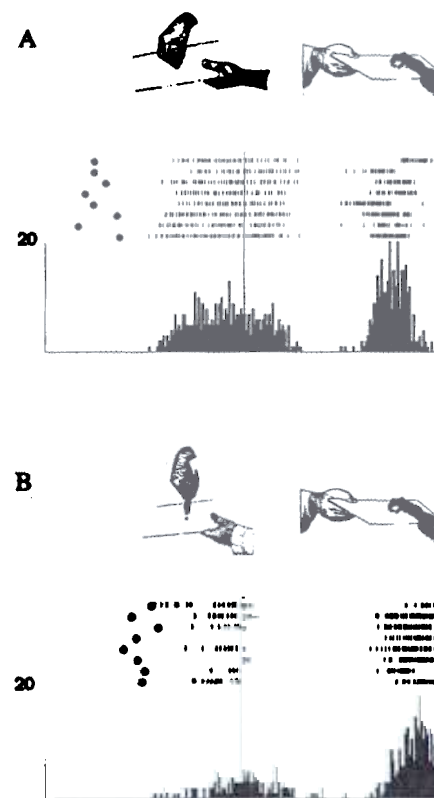


FIGURE 38.7 Example of the visual and motor responses of an F5 mirror neuron. The behavioral situations during which the neural activity was recorded are illustrated schematically above rasters. (A) A tray with a piece of food placed on it was presented to the monkey; the experimenter made the grasping movement toward the food and then moved the tray with the food toward the monkey, which grasped it. The neural discharge was absent when the food was presented and moved toward the monkey. In contrast, a strong activation was present during grasping movements of both the experimenter and the monkey. (B) As in (A), except that the experimenter grasped the food with pliers. Note the much weaker response when the observed grasping was performed with a tool. Rasters and histograms are aligned (vertical bar) with the moment in which the experimenter touched the food. Dots indicate the beginning of the trials. Abscissae: time. Ordinates: spikes/bin. Bin width: 20 ms. (From Gallese et al., 1996.)

tions made using tools either did not activate the neurons or activated them only very weakly (see figure 38.7).

The observed hand actions most effective in triggering the neurons were grasping, manipulating, and placing. More than half of neurons, among those activated by the observation of hand action, were active during the observation of one action only. The remainders responded to two or, rarely, three of them. Some neurons were selective not only to the general action aim (e.g., grasping) but also to how the action was performed, selectively firing during the observation of one particular type of grip (e.g., precision grip, but not whole-hand prehension).

There was a large amount of generalization in terms of the precise physical aspects of the effective agent. For many neurons, the precise hand orientation was not crucial for activation. Similarly, in most cases, the distance from the monkey at which the action was executed did not influence the response. For most neurons, the effect was the same when the experimenter used the right or the left hand. In one third of tested neurons, however, the discharge consistently was stronger when the action was made by one hand instead of the other.

As far as the objects targets of the observed action are concerned, their significance for the monkey did not influence the neuron discharge. The responses to meaningful objects like food were the same as those to 3-D solids. The sizes of the objects, target of the action, were relevant in one third of the recorded neurons. In these cases, neurons were visually activated only when the object of the effective observed action had a specific size. The selectivity was related to the real size of the object and not to its size on the retina. It is likely, however, that this selectivity was not due to the visual characteristics of the objects, but to the grip that their size evokes. Experiments to dissociate these two variables have not been carried out yet.

led using a second monkey as the agent of the action. Although the second monkey grasped food and ate it, the first monkey (the monkey from which neurons were recorded) observed its action passively.

MIRROR NEURONS PROPERTIES The visual stimuli most effective in triggering mirror neurons were found to be actions in which an agent (another monkey or an experimenter) interacts with an object using either the hand or, more rarely, the mouth. Object presentation, including interesting stimuli such as food items or the sight of faces or body movements were ineffective. Similarly, ac-

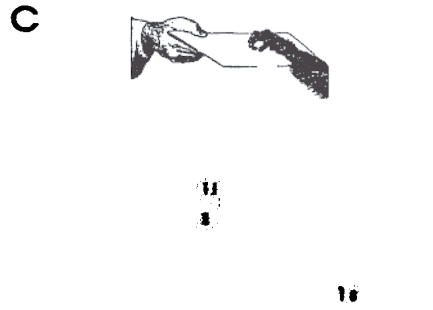
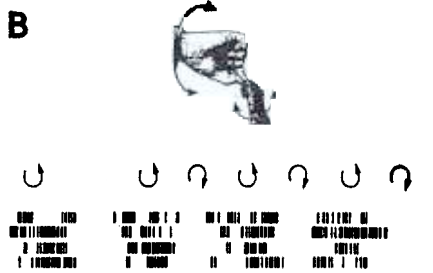


FIGURE 38.8 Example of the visual and motor responses of a highly congruent F5 mirror neuron. The behavioral situations during which the neural activity was recorded are illustrated schematically above neural records. Four continuous recordings are shown in each panel. (A) The monkey observes the experimenter rotating his hands around a small piece of food 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, which opposes the experimenter movement by rotating its wrist in the opposite direction. (C) The monkey grasps a piece of food using a precision grip. Small arrows above the records in (A) and (B) indicate the rotations direction. (From Rizzolatti et al., 1996a.)

precision grip). For other neurons, the congruence was broader. For them, the motor requirements (e.g., precision grip) usually were more strict than the visual ones (any type of hand grasping). An example of a highly congruent mirror neuron is shown in figure 38.8.

OTHER AREAS RESPONDING SELECTIVELY TO BIOLOGICAL STIMULI Neurons responding to complex biological stimuli had been described previously in the macaque brain. A series of studies showed that neurons that discharge selectively to the presentation of faces or hands are present in the inferotemporal lobe (Gross, Rocha-Miranda, and Bender, 1972; Perrett, Rolls, and Caan, 1982; Desimone et al., 1984; Rodman, O'Scalaidhe, and Gross, 1993) and in the prefrontal lobe below the principal sulcus (Pigarev, Rizzolatti, and Scandolara, 1979; O'Scalaidhe, Wilson, and Goldman-Rakic, 1997). Neurons responding to complex biological visual stimuli such as walking or climbing also were reported in the amygdala (Brothers, Ring, and Kling, 1990). Even more relevant to the present issue is the work of Perrett and co-workers (Perrett, Rolls, and Caan, 1982; Perrett et al., 1989, 1990). These authors showed that in the lower bank of the superior temporal sulcus (STS), there are neurons selectively activated by the observation of hand-object interactions. These properties resemble the visual properties of F5 mirror neurons: both STS and F5 mirror neurons code the same types of actions; they both generalize their responses to the different instances of the same action; and neither are responsive to mimicked hand actions without the target object. However, the distinctive feature of F5 neurons—and, so far, their uniqueness—resides in the fact that they discharge also during active movements of the observer: an observed action and action actively made produce the same neural pattern of activation.

The presence of two brain regions, neurons of which are endowed with similar visual properties, raises the question of their possible relationship. A possibility is

that STS and F5 represent distinct stages of the same system. The STS neurons provide an initial "pictorial" description of an action that is then fed (through an intermediate step in the posterior parietal cortex or in the prefrontal lobe) to area F5, where this description is matched with the pattern responsible for the execution of the same action.

THE MIRROR SYSTEM IN HUMANS The first evidence that a mirror system exists in humans was provided by Fadiga and associates (1995), who stimulated the motor cortex of normal human subjects using transcranial magnetic stimulation (TMS). The rationale of the experiment was the following. If the observation of an action activates the premotor cortex in humans, as it does in monkeys, then TMS should induce, during action observation, an enhancement of motor-evoked potentials (MEPs) recorded from the muscles that are active when the observed action is executed. The results confirmed the hypothesis. During the observation of grasping movements, a selective increase of MEPs was observed in the muscles that the subjects used for grasping objects.

Although these data indicate that an action execution/observation matching system exists in humans, they do not give information on the circuits underlying it. Data on this issue were provided by two positron-emission tomography (PET) experiments (Rizzolatti et al., 1996b; Grafton et al. 1996) and, more recently, by a neuromagnetic study (Hari et al., 1998). The two PET experiments differed in many aspects, but both had a condition in which subjects observed the experimenter grasping an object. In this condition, there was an activation of the STS, the inferior parietal lobule, and the inferior frontal gyrus (area 45). All activations were in the left hemisphere. The neuromagnetic study (Hari et al., 1998) was focused on the precentral motor cortex, the basic rhythm of which desynchronizes during active hand movements (Salenius et al., 1997). The results showed that grasping observation produced a similar desynchronization in the absence of any movement. The grasping observation-related desynchronization most likely reflects an activation of motor cortex due to an input to it coming from the inferior frontal gyrus or other premotor areas. The alternative interpretation, that mirror neurons also are present in the precentral motor cortex, is rather unlikely considering their absence in monkey area F1 (area 4) (Gallese et al., 1996).

Thus, the cortical areas active during action observation in humans match well those active in the monkey in the same conditions. In addition to the aforementioned areas containing neurons responding to meaningful biological stimuli, preliminary evidence from our laboratory shows that mirror neurons are present in inferior

parietal cortex (Fogassi et al., 1998). Note also that there is a growing consensus that F5 is the monkey homologue of Broca's area, or of part of it (Von Bonin and Bailey, 1947; Petrides and Pandya, 1994; Preuss, Stepniwaka, and Kaa, 1996; and Rizzolatti and Arbib, 1998).

Taken together, these data indicate that a system matching action observation and action execution is present in humans as in monkeys. This system includes frontal, parietal, and temporal lobe areas.

POSSIBLE FUNCTION OF MIRROR NEURONS Primates are social animals living in continuous mutual relationship with conspecifics. Macaque monkeys live in groups characterized by active and intense social interactions, such as parental care, mating, and grooming that usually are disciplined by a well-delineated hierarchical organization. Therefore, it is crucial for each member of a given social group to be able to recognize the presence of another individual performing an action, to discriminate the observed action from others, and to "understand" the meaning of the observed action to react appropriately to it.

The observation of actions made by other individuals has another important function, that of learning their actions. When we learn a new motor skill, we observe and reproduce again and again the same sequence of actions that the teacher is displaying in front of us. The goal is to achieve as much as possible a match between the teacher-skilled motor behavior and our clumsy approximations of it. Evidence from developmental psychology demonstrates that in humans, the capacity to imitate is displayed soon after birth (Meltzoff and Moore, 1977). However, there is controversy about whether monkeys are able to learn by imitation; many authors maintain that a true learning by imitation is present, among primates, only in humans (see references in Galef, 1988; Whiten and Ham, 1992; Tomasello, Kruger, and Ratner, 1993; Byrne, 1995; Galef, 1998).

How do we recognize and imitate actions? One possibility is that action understanding and imitations require a complex cognitive description of the observed act. The existence of the mirror system suggests, however, another and simpler possibility. Everybody agrees that when an individual starts an action, he or she knows (predicts) its consequences. This knowledge is the result of an association between the schema of that action (the aforementioned potential action coded in the premotor cortex) and the consequences of this action. Thanks to mirror neurons, this knowledge can be extended to actions performed by others. When the observation of an action performed by another individual activates neurons that represent that action in the observer's premotor

cortex, the observed action is recognized because of the similarity (or even identity) of the evoked representation to that internally generated during its active programming.

Thus, we propose that the mirror system is a basic system for recognition of action. Both monkeys and humans use it for this purpose. In addition humans probably use this system also for action imitation (Jeannerod, 1994). If, as maintained by many, monkeys are unable to imitate actions made by other individuals, this would suggest that, although endowed of a mechanism that generates internal copies of actions made by others, they are unable to use them for replicating those actions. This would suggest that the intentional use of internal copies of actions developed only late in evolution.

Conclusions

What is the use of the motor system? The classical answer to this question is undoubtedly the one cited in the introductory section: "The motor system exists to translate thought, sensation and emotion into movement." The data reviewed in this chapter lead to a different and broader view. In primates, the aim of the motor system is to create internal copies of actions and to use these internal copies for generating actions as well as for understanding motor events.

According to this view, there are "vocabularies" of motor actions at the core of the cortical motor system. Neurons forming these "vocabularies" store both knowledge about an action and the description, at least in general (nonparametric) terms, of how this knowledge should be used. The ensemble of neurons related to a given action forms the global motor schema of that action. When an appropriate stimulus is presented, the relevant schema is activated. This does not imply that the action occurs any time a motor schema is activated. The activation of a motor schema determines only the appearance of an internal copy of that action that may be executed.

In the vocabulary of F5, there are two sets of visuomotor neurons: canonical neurons and mirror neurons. Canonical neurons together with neurons located in the parietal lobe area AIP form a circuit that transforms intrinsic object properties into hand action. They are automatically (regardless of animal intention to act) activated in response to appropriate stimulus presentation. The movements do not necessarily follow this activation. The way in which this internal copy, a potential action, is transformed into a real action currently is not known. Our suggestion is that the lateral parietofrontal circuits are under control of mesial motor areas (Rizzolatti et al., 1990; Rizzolatti, Luppino, and Matelli, 1996). Among

these, particularly suitable for this control role is area F6, which receives a massive input from prefrontal cortex (Luppino et al., 1993; Lu, Preston, and Strick, 1994). When internal and external contingencies are such that it is both desirable and feasible that a potential action becomes a real action, the control exerted by mesial areas is removed and the action may unroll.

From the existence of an internal copy of actions stems the second function of the motor system, that of matching an observed action onto the internal motor copy of the same action. The presence of a common code for a received message (in the case of mirror neurons, actions made by others) and for an action actively emitted by the observing individual gives a cue on how individuals can understand the "pictorial" description of the inferotemporal and parietal areas. The evidence we present concerns event recognition but it is likely that in early periods of life, the same mechanism is used also for giving meaning to other types of percepts (see Rizzolatti and Gallese, 1997). These considerations, although at the moment purely hypothetical, appear to be extremely fascinating because they open the possibility to approach neurophysiological issues that, like object semantics, were traditionally the domain of philosophical inquiry.

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39 Neural Mechanisms for Learning of Sequential Procedures

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ABSTRACT Acquisition of procedural skill requires long-term practice with repeated trial-and-error processes during which acquisition of knowledge (what to do) gradually is replaced with acquisition of skill (how to do). Using a visuomotor sequence task with trial-and-error processes for macaque monkeys and humans, the authors have shown that multiple brain areas contribute to different stages and different aspects of procedural learning. The frontal cortex (particularly the pre-supplementary motor area [SMA]) and the anterior part of the basal ganglia contribute to the initial stage of learning, in which knowledge for the procedure is acquired. The authors' data also suggested that procedural skill is acquired simultaneously, in which the SMA plays an important role. In contrast, the posterior part of the basal ganglia and the dentate nucleus of the cerebellum contribute to the long-term learning stage, in which the procedure is executed implicitly with a chain of anticipatory movements.

Based on their results and the results from other laboratories, the authors propose a hypothetical scheme in which a sequential procedure is learned independently by two parallel mechanisms in the cerebral cortex that use the visual and motor coordinates. Both of them are supported by the basal ganglia and the cerebellum: The basal ganglia provided them with reinforcement signals, and the cerebellum provided them with timing information. The proposed neural architecture would operate in an effective and flexible manner to acquire multiple sequential procedures.

Intelligence is based on the ability to learn a complex sequence of movements, as implicated in the usage of tools (Matsuzawa, 1996) and languages (Kuhl, 1994). How we learn such sequential procedures has been a long-standing objective of psychology and currently is a major topic in neuroscience. However, our understanding is far from complete. We hardly are able to pinpoint the brain structures that are critical for the sequential procedural learning. A consensus among neuroscientists is that the brain regions that are critical for declarative memory, including the hippocampus, are not critical for procedural learning or memory (Squire and Zola, 1996). Therefore, the procedural memory has been characterized by exclusion—that is, what is left out of the declara-

tive memory mechanisms. Interestingly, this is the very reason why many neuroscientists currently are interested in disclosing the mystery of procedural learning.

In this review, we first describe the current status of the research on procedural learning, then summarize our study on monkeys and humans, and finally propose a neural network model as an attempt to integrate results from our and other laboratories.¹

Brain regions that are implicated in procedural learning

As summarized in table 39.1, a number of brain regions have been shown to be involved in different types of learning. Interestingly, learning of sequential procedures currently is a major issue in studies using human subjects, but it rarely has been studied using animal subjects. Sequential procedures have been used in animal studies only after they have been learned to study the control mechanism of sequential movements (Tanji and Shima, 1994).

However, many of the human studies, especially imaging studies using positron-emission tomography (PET) or functional magnetic resonance imaging (fMRI), have focused on learning of sequential movements, such as the serial reaction time (SRT) task (Nissen and Bullemer, 1987). Common to the results of these studies was that several brain areas were active concurrently during learning, including the cerebral cortex, the basal ganglia, and the cerebellum. It has been proposed that there are different stages in learning to which different brain regions contribute (Karni et al., 1998; Petersen et al., 1998; Shadmehr and Brashers-Krug, 1997).

However, it still was unclear whether these brain regions actually contribute to the learning and how they interact with each other during learning. Crucial to answering this question was: (1) to identify the brain regions that were active with learning and (2) to manipulate the activity of each region to see whether learning and retention of memory were disrupted. Our strategy was to combine animal and human experiments

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