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Visuomotor neurons: ambiguity of the discharge or 'motor' perception?

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Abstract

The cortical motor system has been classically considered as the unitary, output stage of the brain processing of sensory information. According to this idea, the motor cortex — the acting brain — receives the result of the perceptual processing (visual, acoustical, tactile, etc.) elaborated by the 'associative cortex'. During the last two decades this perspective has been challenged by a series of anatomical, hodological, and neurophysiological data. This converging evidence delineates a dramatically changed picture. Far from being unitary, the cortical motor system appears to be constituted by a constellation of distinct areas, each of those endowed with specific functional properties and linked by reciprocal connections with distinct sectors of the parietal cortex. Furthermore, several 'motor' neurons in addition to their motor discharge, are also activated by somatosensory and visual stimulation (somatomotor and visuomotor neurons). In the present paper we will discuss the functional properties of those sensorimotor neurons located in the ventral part of the monkey premotor cortex. On the basis of electrophysiological data, we will propose that the apparent parodox stemming from the coexistence within the same neuron of motor and sensory properties can be solved by postulating that the motor system not only *executes* actions but also internally *represents* them in terms of 'motor ideas'. These motor ideas may provide the neurobiological basis for space representation, understanding of actions made by others and, possibly, semantic categorization of objects. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Premotor cortex; Mirror neurons; Single neuron recording; Action and perception

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1. Introduction

One of the strongest dogmas in clinical neurophysiology is that conveyed by the simiusculi and homunculi of Woolsey (Woolsey, 1958) and Penfield (Penfield and Rasmussen, 1950). No one among all neuroscience textbooks fails to represent the suggestive picture of the two dwarfs with enormous hands and mouths: the larger one lying upside down just in front of the Rolandic fissure, the smaller one sleeping supine on the mesial cortex of the frontal lobe. Unfortunately, despite the benefits given by this picture to thousands of students to memorize the fundamental concepts of somatotopic representation of movements, the homunculi favored the idea that the motor system is formed by only two areas: the primary motor cortex (MI); and the supplementary motor cortex (MII) (Fig. 1). This functional description of the motor cortex was also supported by some neuroanatomical data: the frontal motor cortex is cytoarchitectonically characterized by an agranular structure with no clear-cut differences among its different sectors. Thus, the optimal criteria for the partition of the frontal lobe into different areas were strongly debated since the very beginning of the modern neuroanatomy. In 1909 Brodmann (Brodmann, 1909), on the basis of the distribution of pyramidal cells, considered the frontal motor cortex of primates as formed by two areas (4 and 6, Fig. 1) which almost completely overlapped with the extension of the two 'homunculi'. For many years, despite the fact that already in 1919 Vogt and Vogt considered the subdivision of the motor cortex in only two areas insufficient (Vogt and Vogt, 1919), the motor (area 4, considered the main source of corticospinal projections) and premotor (area 6, considered involved in motor preparation, mainly of proximal movements) areas were considered by neurophysiologists as an acceptable description of the 'state of the art'.

The reason why this view gained so large a consensus can be explained in two ways: First, it gave a simple account of a complex problem. Second, it perfectly agreed with the dominant idea of a functionally unitary motor system. According to this idea the motor cortex, the 'acting brain', was considered to be the final output stage after the processing of sensory perceptions (visual, acoustical, tactile, etc.) elaborated by the huge 'associative cortex'.

Fig. 1. Lateral and mesial view of the macaque monkey brain. Light gray and dark gray shading indicate area 4 and area 6 of Brodmann, respectively. The two simiusculi correspond to the somatotopic representation of movements in the primary motor cortex (MI) and in the supplementary motor cortex (MII) as described by Woolsey (1958).

During the last two decades this 'classical' notion of the motor system has been challenged by a series of experimental evidence:

1. According to cytoarchitectonical (Matelli et al., 1991; Petrides and Pandya, 1994), histochemical (Matelli et al., 1985) and neurochemical (Matelli et al., 1996) studies, the agranular part of the frontal lobes *is formed by a constellation of distinct areas*. Fig. 2 shows a modern parcellation of the agranular frontal cortex based on the work of Matelli et al. (see for review Rizzolatti et al., 1998). Note that while F1 approximately corresponds to a shrinked version of Brodmann area 4 (the precentral motor cortex, corresponding to Woolsey's MI), Brodmann area 6 appears to be formed by a mosaic of different areas. Areas F2 and F7 form the dorsal sector of area 6, areas F4 and F5 the ventral sector, while areas F3 and F6 are located on the

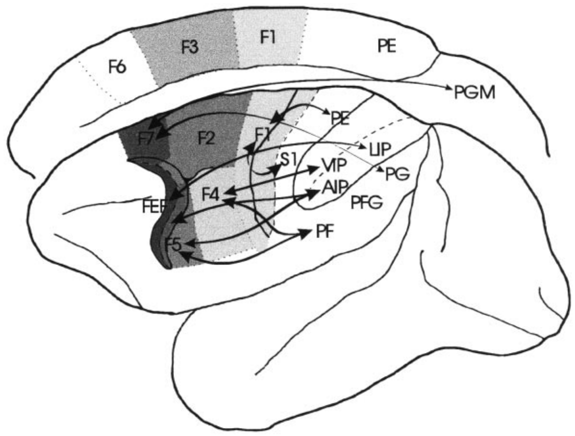

Fig. 2. Lateral and mesial view of the macaque monkey brain showing the main parieto-frontal circuits of the lateral convexity. Gray shading of different intensity indicates the cytoarchitectural and cytochrome oxidase areas (F1-F7) forming the agranular frontal cortex in the subdivision made by Matelli et al. 1985, 1991. FEF refers to frontal eye fields. Area PE corresponds to the convexity of the superior parietal lobule; areas PF, PFG and PG are subdivisions of the convexity of the inferior parietal lobule; areas AIP, LIP and VIP are subdivisions of the lateral bank of intraparietal sulcus. SI refers to primary somatosensory area. Note that both arcuate and intraparietal sulci are opened to show areas buried inside of them.

mesial convexity, buried inside the interhemisferic fissure. Area F3 broadly corresponds to the Woolsey's supplementary motor cortex (MII). This multiple subdivision of the agranular frontal cortex is also supported by hodologic considerations. Almost all frontal motor areas have their main source of connection in the parietal lobe, where a similar 'mosaic-shaped' organization is present. The frontal and parietal 'mosaics' are bidirectionally connected through a series of parallel circuits (see Rizzolatti et al., 1997, 1998) (see Fig. 2).

2. The electrophysiological study of neurons forming these parietal–frontal circuits (see Rizzolatti et al., 1997, 1998) suggests their possible involvement in the transformation of sensory information into action, and show that frontal and parietal areas are organized in an effector specific (i.e. arm, hand, head, eyes) and are not modality specific (vision, somesthetic perception, etc.) way. This observation leads to two orders of consequences: First, the Woolsey's idea that the frontal cortex contains only two somatotopic motor representations is wrong. Fig. 3 schematically show the somatotopic maps present in the frontal lobe. Second, the old concept stating that different functions are segregated in different areas is probably too simplistic. If from one side is certainly true that cortical areas, and mainly those involved in 'primary' perception, are characterized by a predominant function (we are not aiming here to reinforce the 'allistic' concept of Flourens, 1824), the anatomical and functional organization of the parietal and frontal 'mosaics' suggests some new possible insights on concepts like movement, sensation and perception. These brain functions appear to be not an exclusive prerogative of specifically 'dedicated' areas, but are represented multiply in cortical areas. It now appears clear that *spatial positions, objects physical characteristics and, possibly, object semantics, have multiple descriptions in the brain, each with different purposes, according to the different effectors acting in a particular context*. Space, for instance, although introspectively perceived as unitary, is not represented in a single cortical area as a multipurpose map. On the contrary, there is growing experimental evidence that there are many spatial maps at least as many are the motor effectors that act in the environment (see Rizzolatti et al., 1997). Accordingly, the spatial map for eye movements is organized differently in terms of coordinates and stimulus specificity with respect to those maps used for body parts mobilization.
3. *Several neurons located in the agranular frontal cortex, in addition to their typical motor related activity, discharge also during passive stimulation*. This sensorimotor coupling is very often effector specific. Thus, neuronal responses to deep tactile and proprioceptive stimulation are evoked in the precentral cortex (see for example Wong et al., 1978), face, arm and body superficial tactile stimulation excite area F4 neurons (Rizzolatti et al., 1981a; Gentilucci et al., 1988; Fogassi et al., 1996a,b); passive arm joint mobilization activate arm-

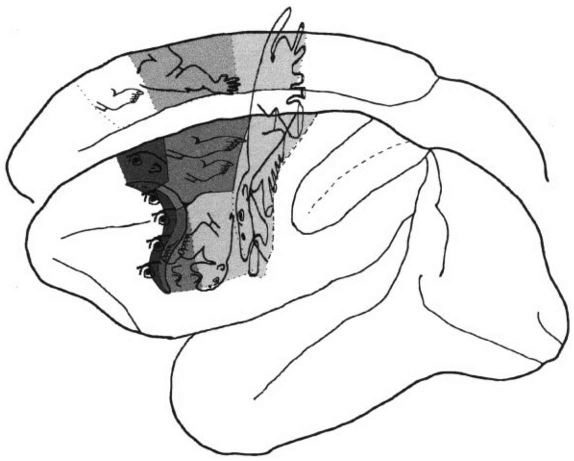

Fig. 3. Lateral and mesial view of the macaque monkey brain showing in a schematic way the multiple somatotopic representation of movements in the agranular frontal cortex. Other conventions are as mentioned in Fig. 2.

related neurons of area F2 (Fogassi et al., in press); and finger passive stimulation correlates with the discharge of area F5 neurons (Rizzolatti et al., 1988). In addition, mainly in the ventral part of the premotor cortex, there are neurons that discharge also to visual stimulation (Rizzolatti et al., 1981b, 1988; Gentilucci et al., 1983, 1988; Fogassi et al., 1996a,b; Gallese et al., 1996; Murata et al., 1997). This last point raises some fundamental questions about the nature of the discharge of these 'motor neurons'. If these cells are activated both during action and during 'perception' what is the output message they send? Which is, in terms of brain representation, the possible meaning underlying this apparently ambiguous behavior? In the present article we will focus mainly on these questions, by reviewing some recent neurophysiological data characterizing visuomotor responses in premotor neurons.

2. Motor and visual responses coexist in the ventral premotor cortex

One of the most fascinating discoveries in neurophysiology in the last two decades is that neurons located in a frontal region classically considered as motor, *in addition to their motor discharge, responded also to the presentation of visual stimuli*. Neurons with this property mainly pertain to FEF (Bruce and Golberg, 1985) area F4 and F5 (Rizzolatti et al., 1981b, 1988; Gentilucci et al., 1983, 1988) that, taken together, represent the main target for the inferior parietal lobule projections conveying visual information. As in the case of somatosensory–motor coupling (see above), visual responses of F4 and F5 neurons appear to be related to the effectors that are somatotopically represented in these areas. In the following sections we will describe separately the physiological properties of these two areas.

2.1. General properties of area F4

Area F4 forms the caudal part of ventral premotor cortex (see Fig. 2). Intracortical microstimulation performed in this area reveals a rough somatotopic representation of neck, proximal arm, trunk and face/mouth movement (Gentilucci et al., 1988). Although the discharge of F4 neurons during the execution of trunk and neck movements is difficult to examine in normal laboratory conditions because the animal head is kept fixed during electrophysiological recordings, the available data show a good correlation between active movement and microstimulation results (Gentilucci et al., 1988). In addition to the motor discharge, the large majority of F4 neurons respond also to sensory stimulation (Gentilucci et al., 1988; Fogassi et al., 1996a,b). On the basis of these responses they were subdivided into two classes: somatosensory neurons and bimodal (somatosensory and visual) neurons. Somatosensory neurons have superficial tactile receptive fields located on face, chest and arm. The size of tactile receptive fields may vary, but generally ranges from a few centimeters to a complete hemiface (Fogassi et al., 1996a,b).

Somatosensory properties of bimodal neurons are almost the same of the purely somatosensory ones but, in addition, these neurons discharge when a tridimensional visual stimulus is introduced inside the space around the animal. Neuronal responses are enhanced if the stimulus is moved towards the neurons' tactile receptive field. In Section 2.2 we will examine the basic properties of bimodal F4 neurons.

2.2. Visual properties of area F4

The regions of space around the animal whose visual stimulation with three-dimensional objects causes a modulation of neuronal discharge is a visual receptive field: these fields are very often in register with the tactile receptive field of the same neuron, are clearly delimited in depth (ranging from 1–2 cm to approx. 40–50 cm) and their stimulation produces a highly reliable neuronal response, constant among trials. If the stimulus is moved outside the visual receptive field border, no response is evoked from the neuron. Fig. 4 shows localization and extension of tactile and visual receptive fields of some typical F4 neurons.

Electrophysiological studies of F4 neurons visual responses showed that visual receptive fields remain anchored to the tactile receptive fields independently of where the animal directs its gaze (Gentilucci et al., 1983; Fogassi et al., 1996a). Fig. 5 shows the behavior of a typical F4 neuron tested in a paradigm aimed to determine if visual receptive fields move with the eyes (retinotopic code) or if they remain anchored to the body part from which they originate (somatocentric code). In the first condition (A1) the monkey is looking straight ahead (the asterisk on the picture represent the fixation point) and an approaching stimulus (black arrow) is moved at constant velocity inside the visual receptive field (gray area). The histogram of the discharge shows a clear response that starts when the stimulus is approximately 40 cm from the animal. Condition A2 shows the same stimulus trajectory but with the monkey gaze deviated 30° to the left. In B1 and B2 conditions the visual stimulus is moved outside the receptive field and no responses are recorded from the neuron, also when the gaze is deviated towards the stimulus (B2). This last condition is the critical one that allows to determine whether F4 visual receptive fields are coded in a non-retinotopic coordinate system: In the case of a retinotopically coded visual receptive field, the gaze deviation towards the visual stimulus should be accompanied by an analogous deviation of the receptive field revealed by the presence of neuron discharge in this condition. More than seventy F4 neurons were studied with this paradigm and the results showed that a large proportion of them (70%) have a receptive field anchored to the tactile one (see Fogassi et al., 1996a).

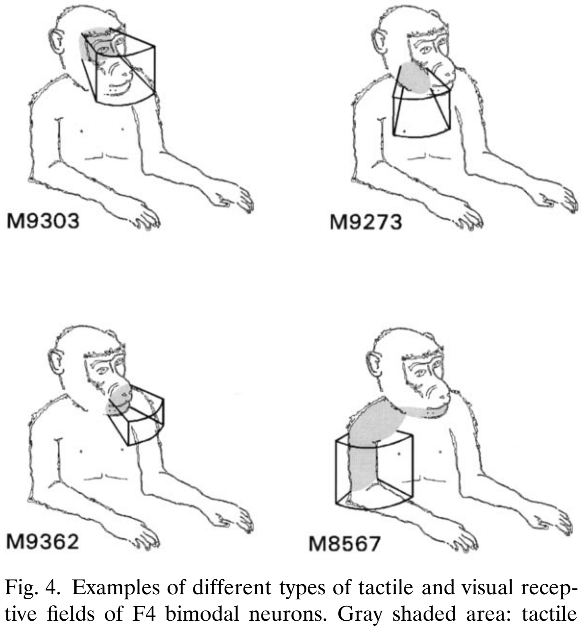

Fig. 4. Examples of different types of tactile and visual receptive fields of F4 bimodal neurons. Gray shaded area: tactile receptive fields. Solid around the tactile receptive fields: visual receptive fields.

An important finding was that the receptive field spatial coordinates do not originate from a single reference point (e.g. on the body mid-line) as it was frequently suggested by theoretical studies, but are anchored to different body parts (Gentilucci et al., 1988). The hypothesis of a multiplicity of spatial coordinate systems recently received further support from the work of Graziano et al. (Graziano et al., 1994, 1997; Graziano and Gross 1998). In experiments similar to the one described above, these authors mapped the neuron visual receptive field and then moved the body part (e.g. arm) around which the field was located. They found that the visual receptive field moved together with the body segment. It is therefore clear, that there is not one single reference point for skeletal movements, but a multiplicity of different reference points depending on

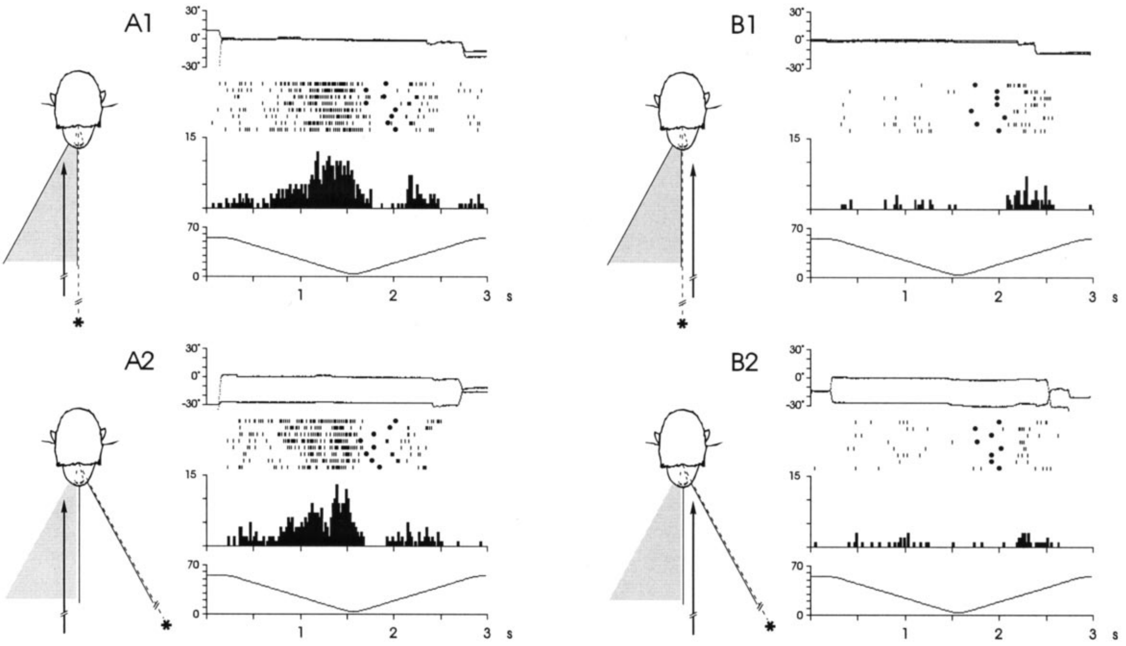

Fig. 5. Bimodal F4 neuron with somato-centered visual receptive field. Each panel shows (from top to bottom) horizontal and vertical eye movements, rasters illustrating neural discharge during individual trials, the response histogram (abscissae: time; ordinates: spikes/bin, bin width 20 ms) and variation in time of the distance between the approaching stimulus and the monkey's head. The descending part of the curve indicates movement of the stimulus toward the monkey, the ascending part movement of the stimulus away from the monkey (abscissae: time in s; ordinates: distance in cm). The tactile receptive field was located on the right hemiface. The visual receptive field was in register with the tactile field. See text for the description of the experimental paradigm.

the location of the tactile/visual receptive fields. Thus, head centered, arm centered, chest centered coordinate systems are possible.

The studies of area F4 were mainly directed to clarify the sensory properties of F4 neurons. In few neurons, in addition to sensory properties, motor properties were also investigated. A good congruence was found between the visual receptive field location of a given neuron and the spatial position towards which the hand had to be moved in order to excite that neuron (Fogassi et al., 1996b).

2.3. Functional meaning of F4 visuomotor responses

The presence of neurons in F4 that discharge both in response to visual stimulation, and during monkey's active movements raises the problem of the nature of the visual responses. Several hypotheses can be made.

The first hypothesis, which is the most obvious (and conservative), considers the visual discharge of F4 neurons a kind of motor preparation for an impending action on the stimulus. However, this hypothesis seems quite implausible because the presence of the visual discharge does not depend on the nature of the stimulus: pleasant, neutral or unpleasant stimuli (that obviously evoke completely different behaviors) are all effective in producing the same neuron response.

The second hypothesis postulates that F4 visual responses are really visual and code space in visual terms. In other words, given a reference point (e.g. the body part on which the visual receptive field is anchored), the neurons signal the location in space of a given object by using a sort of geometrical coordinate system mapping the visual space. This interpretation asserts that the visual responses of F4 neurons are truly sensory. The main arguments in favor of this interpretation are the strict temporal link between stimulus presentation and the onset of neuron discharge, the response constancy and the presence of visual receptive fields.

The third hypothesis states that the visual discharge of F4 neurons reflects a 'potential action' directed towards a particular spatial location. The presentation of a visual stimulus evokes automatically one of these 'potential actions', which, regardless of their execution, maps the position in space of the stimulus in motor terms. In favor of this hypothesis is the fact that area F4 is a premotor area directly connected with the primary motor cortex and to the spinal cord (Matelli et al., 1986; He et al., 1993), and the suspect that 'space' is not a 'perceptual' category but is generated as a consequence of a motor interaction with the environment (as suggested already by several psychophysics of the last century, see e.g. Mach, 1896). These elements appear to favor the idea that F4 contains a store of potential movements (a sort of 'motor vocabulary') for bringing the head or the arm towards specific spatial locations. Furthermore, from a more general point of view, with respect to the 'visual' hypothesis, the 'motor' interpretation offers a better or, at least, a more economical explanation for the location of spatial receptive fields around the body. If the 'visual' interpretation were correct, one would have to postulate an 'ad hoc' complex visual mechanism able to eliminate visual information coming from points outside the peripersonal space. In contrast, the three-dimensional properties of premotor receptive fields are easily accommodated by a 'motor' interpretation. According to this view, are the movements that progressively carve out a working space from an undifferentiated visual information.

2.4. General properties of area F5

Area F5 forms the rostral part of ventral premotor cortex (see Fig. 2). Intracortical microstimulation of area F5 and single neurons recordings during active movement have shown that in this area there is a representation of hand and mouth movements (Okano and Tanji, 1987; Rizzolatti et al., 1988).

The great majority of F5 'hand' neurons discharge during goal-directed actions such as grasping, manipulating, tearing, holding (Rizzolatti et al., 1988). F5 neurons do not discharge during similar fingers and hand movements when made with other purposes (e.g. scraping, pushing away, etc.). Furthermore, many F5 neurons become active during movements that share the same goal but are performed with different effectors. For example, several grasping neurons discharge when the monkey grasps an object with its right hand, with its left hand or with the mouth. It is obvious that in this case a description of neuron behavior in terms of elementary movements makes little sense.

The mostly represented F5 neurons are 'grasping neurons'. These neurons typically begin to discharge before the contact between the hand and the object. Some neurons are more active during the opening of the fingers that precedes the closure phase, some discharge during finger closure and some others discharge during the whole movement, from the beginning of fingers opening until their contact with the object. This temporal relation between grasping movement and neuron discharge varies from neuron to neuron. Furthermore, many grasping neurons discharge in association with a particular type of grip. Most of them are selective for one of the three most common grip types of the monkey: precision grip, finger prehension and whole hand prehension. Sometimes there is also specificity within the same general type of grip. For instance, considering the whole hand grasping, the prehension of a sphere, which requires the opposition of all fingers, is coded by neurons different from those coding the prehension of a cylinder, which requires the opposition of all fingers but the thumb.

Taken together, the functional properties of F5 neurons suggest that this area stores a set of motor schemata (Arbib, 1981), or, as it was previously suggested (Rizzolatti and Gentilucci, 1988), a 'vocabulary' of motor acts. Populations of neurons constitute the 'words' composing this vocabulary. Some of them indicate the general category of an action (hold, grasp, tear, manipulate). Others specify the appropriate way to better adapt the hand to the grasped object (e.g. precision grip specific neurons vs. whole hand specific neurons).

Finally, other neurons are concerned with the temporal segmentation of the actions (hand opening, fingers closure, object holding). What differentiates area F5 from the precentral motor cortex (F1) is that its motor 'words' are goal directed actions (or fragments of specific goal directed actions), while F1 stores movements regardless of the action context in which they are performed. In comparison with F5, area F1 could be defined as a 'vocabulary of movements'. Note that besides the possible advantage that the F5 vocabulary may give for the execution of hand actions (for a discussion see Rizzolatti and Fadiga, 1998), it gives to the brain a storage of 'action schemata' that, as we will propose below, could also be used for non-strictly motor purposes.

The motor properties of F5 we just described are common to all F5 neurons. However, if one examines F5 neurons that respond also to visual stimuli, it becomes apparent that in F5 there are two completely different categories of visuomotor neurons. *Neurons of the first category discharge when the monkey observes graspable objects* ('canonical' F5 neurons, Rizzolatti and Fadiga, 1998). *Neurons of the second category discharge when the monkey observes another individual making an action in front of it* (Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996). For this peculiar 'resonant' property, we named neurons belonging to the second category 'mirror' neurons (Gallese et al., 1996).

The two categories of F5 neurons are located in two different sub-regions of area F5: 'canonical' neurons are mainly found in that sector of area F5 buried inside the arcuate sulcus, whereas 'mirror' neurons are almost exclusively located in the cortical convexity of F5 (see Fig. 2).

2.5. Visual properties of area F5: 'Canonical' neurons

As firstly described some years ago, in single neuron recording experiments in which a monkey was required to grasp food and other objects, many F5 neurons fired also in response to food/object visual presentation (Rizzolatti et al., 1988). More recently the visual responses of F5 neurons were re-examined using a formal behavioral paradigm, which allowed to separately test the response related to object presentation, during the waiting phase between object presentation and movements onset, and during movement execution (Murata et al., 1997).

The results showed that a high percentage of the tested neurons, in addition to the 'traditional' motor response, responded also to visual presentation of three-dimensional graspable object. Among these visuomotor neurons, two-thirds were selective to one or a few specific objects. Fig. 6a shows the responses of a visually selective neuron. Observation and grasping of a ring produced strong responses. Responses to the other objects were modest (sphere) or virtually absent. Fig. 6b shows the behavior of the same neuron during the mere fixation of the same objects. In this condition the objects were presented in the same way as during the previously described task, but grasping was not allowed and, at the go signal, the monkey had simply to release a key. Note that in this condition the object is totally irrelevant for task execution, which only requires the detection of the go signal. Nevertheless, the neuron strongly discharged at the presentation of the preferred object.

When visual and motor properties of F5 neurons are compared, it becomes clear that there is a strict congruence between the two types of responses. Neurons that become active when the monkey observes objects of small size, discharge also during precision grip. In contrast, neurons selectively active when the monkey looks at a large object, discharge also during action directed towards large objects (e.g. whole-hand prehension).

2.6. Visual properties of area F5: 'Mirror' neurons

'Mirror' neurons constitute a class of F5 visuomotor neurons that become active when the *monkey acts* on an object *and* when it *observes another monkey or the experimenter* making a similar goal directed action (Di Pellegrino et al., 1992; Gallese et al., 1996). 'Mirror' neurons appear, therefore, to be identical to 'canonical' neurons

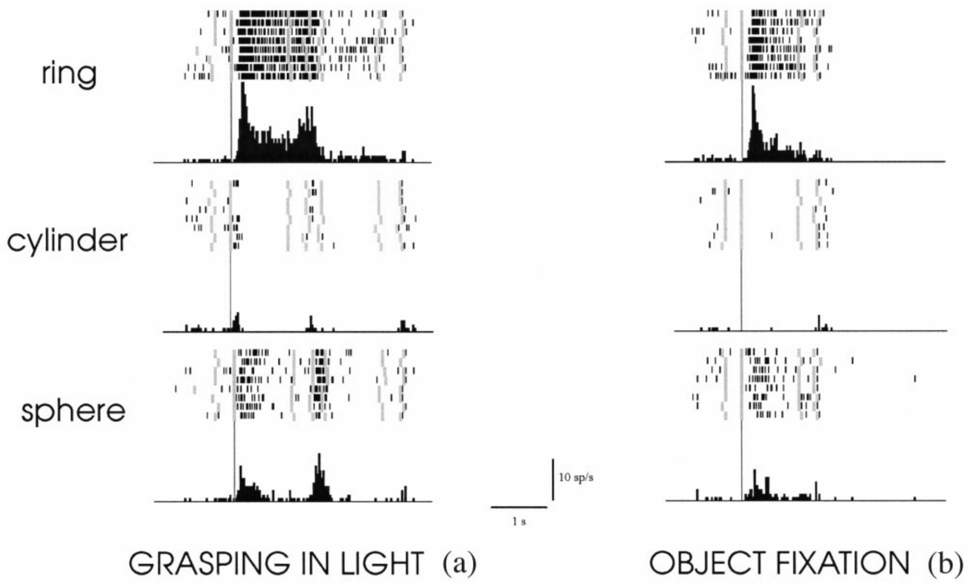

Fig. 6. Example of a selective F5 ‘canonical’ visuomotor neuron. Panels show neural activity recorded during ‘grasping in light’ and ‘object fixation’ tasks with three objects. The behavioral paradigm was the following. The monkey was seated in front of box containing a computer-driven turntable, that allowed the presentation, one at the time, of objects of different shape. A red/green LED was projected onto the object. In the ‘grasping in light’ task the monkey had to fixate a red LED and press a key. Pressing the key determined object illumination. The monkey was required to maintain fixation for 1.0–1.2 s and, when the LED changed color, to release the key, reach for and grasp the object, pull and hold it until the LED changed color again. In the ‘object fixation’ task the monkey had to fixate a green LED and press the key, determining object illumination. The monkey had to maintain fixation for 1.0–1.2 s and release the key when the LED changed color. Rasters and histograms are aligned with key press (vertical bar). Small gray bars in each raster indicate the various task events. The event occurring after the alignment bar indicate the change in LED color, that is the cue for grasping movement onset (a) and for key release (b), respectively. Abscissae: time in s; ordinates: spikes/s.

in terms of motor properties, but they radically differ from them as far as visual properties are concerned (Rizzolatti and Fadiga, 1998).

The visual stimuli most effective in triggering ‘mirror’ neurons discharge are actions in which the experimenter’s hand or mouth interacts with objects. The mere presentation of three-dimensional objects or food is ineffective in evoking mirror neurons discharge. Similarly, actions made using tools, even when conceptually identical to those made by hands (e.g. grasping with a pliers), do not activate the neurons or activate them very weakly.

The observed actions, which most commonly activate mirror neurons, are grasping, placing, manipulating, and holding. Most mirror neurons respond selectively to only one type of action (e.g. grasping). Some are highly specific, coding not only the type of action, but also how that action is executed. They fire, e.g. during observation of grasping movements, but only when the object is grasped with the index finger and the thumb. Examples of mirror neurons are shown in Figs. 7 and 8.

Typically, mirror neurons show congruence between the observed and executed action. This congruence can be extremely strict, that is the effective motor action (e.g. precision grip) coincides with the action that, when seen, triggers the neurons (e.g. precision grip). For other neurons the congruence is broader. For them the motor requirements (e.g. precision grip) are usually stricter than the visual ones (any type of hand grasping).

2.7. Functional meaning of F5 visuomotor responses

Although F5 neurons are indistinguishable for their motor properties (they all discharge during goal directed hand/mouth actions), they can be clearly categorized into two classes according to their visual properties (Rizzolatti and Fadiga, 1998). The first class is formed by 'canonical' neurons that discharge at the visual presentation of graspable objects. The second class is that of 'mirror' neurons that visually discharge when the monkey observes another individual performing hand/mouth actions. Both classes show an interesting congruence between the action coded by a given neuron and the observed — object/action that is able to evoke a visual discharge in that neuron. In other words, a 'canonical' neuron that motorically codes a precision grip is also activated when the monkey looks at a small object. A 'mirror' neuron that motorically codes the same precision grip, becomes active when the monkey looks another monkey (or the experimenter) performing a precision grip in front of it.

How can these findings be explained? It is obvious that the object-related visual responses were not due to unspecific factors such as attention or 'intention to do'. If either of these explanations were true, being attention and 'intention' the same regardless of which is the object presented, the neuron would not have shown object specificity. We are inclined to exclude also the 'motor preparation' interpretation: why canonical neurons discharge at the visual presentation of objects also when the task does not require any successive grasping of the observed object? Why mirror neurons also discharge when the monkey looks at another monkey grasping (and then excluding any possible future reward coming from it)? Furthermore, mirror neurons do not fire when an object (that when grasped or manipulated by the experimenter activate them) is moved toward

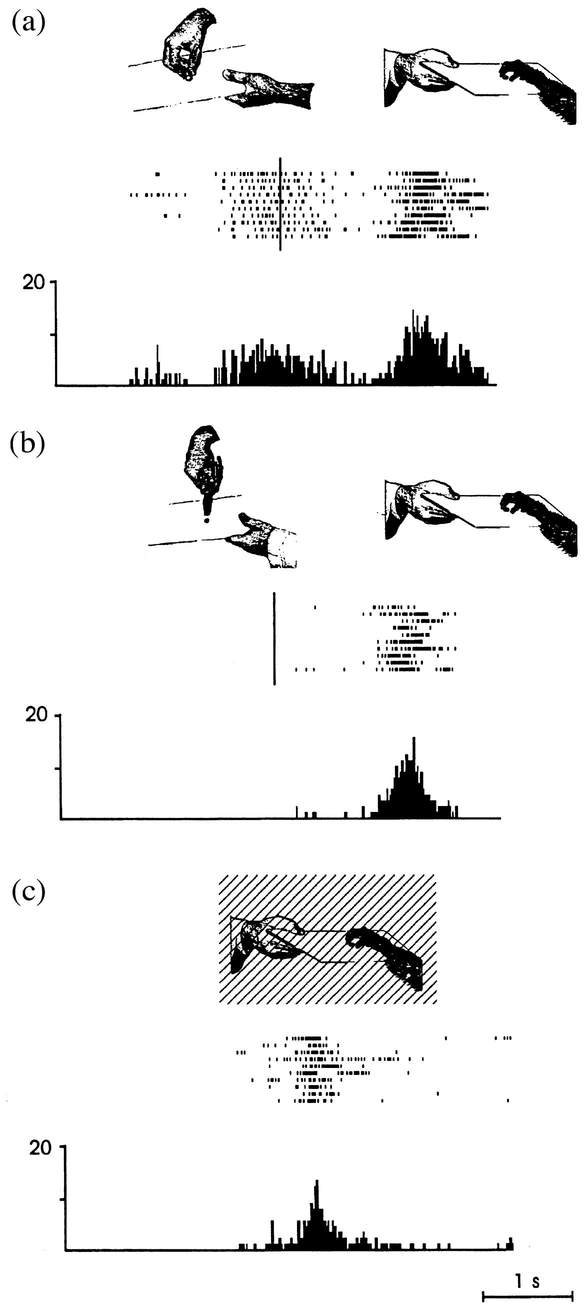

Fig. 7.

Fig. 7. Visual and motor responses of a mirror neuron. In the upper part of each panel is represented the behavioral situation, in the lower panel the neuron response. (a) The experimenter grasps a piece of food held on a support with his hand, then it gives the food to the monkey, that grasps it. The neuron discharges to the observation of grasping and when the monkey grasps. (b) The experimenter grasps food with pliers, then gives the food to the monkey. There is no discharge during action observation. (c). The monkey grasps food in darkness. The neuron discharge is comparable with that observed during grasping in light. In A and B rasters and histogram are aligned with the moment in which the experimenter grasps food (vertical line), in C with the approximate beginning of monkey's grasping movement. Abscissae: time; ordinates: spikes/bin, bin width 20 ms.

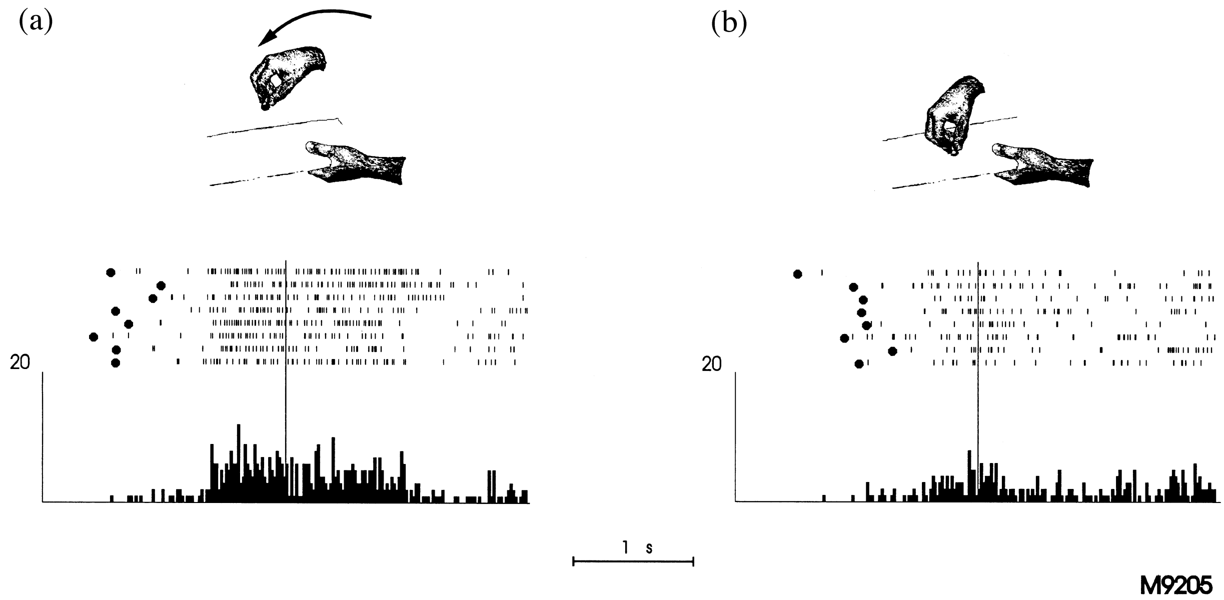

Fig. 8. Visual response of a 'placing' mirror neuron. The neuron discharges when the experimenter places and holds a piece of food on a tray (a), while the response is much weaker when the experimenter grasps a piece of food (b). Conventions as in Fig. 7.

the monkey and made, therefore, more available for an action on it. Motor preparation hypothesis predicts exactly the contrary.

The interpretation we favor for visual discharge in canonical neurons is that, at least in adult individuals, there is a close link between the most common three-dimensional stimuli and the actions necessary to interact with them. Thus, every time a graspable object is visually presented, the related F5 neurons are addressed and the action is 'automatically' evoked. It is interesting to note that in a recent PET study a similar phenomenon was also demonstrated in humans: the presentation of tools or other graspable objects to normal human subjects activates the premotor cortex even when no motor response is required (Grafton et al., 1997). Thus, object-related motor activation appears to represent, in both monkeys and humans, a 'potential' action, an 'idea' of how to act. Under certain circumstances, it guides the execution of the movement, under others it remains an unexecuted representation of it that might be used also for semantic knowledge.

The most likely interpretation of mirror neurons is that their discharge generates an internal representation of the observed action. In other terms, the observed action selects, in the F5 motor vocabulary a congruent 'motor word', a potential action.

It seems plausible that the visual responses of both canonical and mirror neurons address the same motor vocabulary, the words of which constitute the monkey motor repertoire. What is different is the way in which the 'motor words' are selected: in the case of 'canonical' neurons they are selected by object observation, in the case of 'mirror' neurons by the sight of an action. Thus, the visuomotor coupling shown by canonical neurons could be at the basis of the sensorimotor transformation that adapt the hand to a given object. The visuomotor discharge that characterize mirror neurons could be at the basis of action imitation and action understanding (see Rizzolatti et al., 1996; Fadiga and Gallese, 1997).

3. Conclusions

The presence of motor and visual responses in the same neuron may appear, at first glance, paradoxical. What might be the functional meaning of these responses?

The most likely interpretation is that the neuron discharge of visuomotor neurons is neither purely visual nor purely motor: it codes a potential motor action, completely devoid of impending motor requirements or, according to an old terminology, it represents the 'idea' of a specific action. Access to this potential action is possible either automatically (as in the case of visual stimulation of F4 and F5 canonical and mirror neurons) or voluntarily (as in the case of action execution). In other words, according to this interpretation, the discharge of visuomotor neurons may simply mean that a particular action is 'coming in mind' (or in other terms is internally represented), regardless of the future use that the brain will make of it: actions may 'come in mind' when we look at graspable objects, when we look at other individuals acting, when we think to do something and, obviously, when we decide to act. Only in the last case, potential actions are transformed into real ones.

If this interpretation is accepted, a functional homology between the functional organizations of areas F4 and F5 becomes apparent. Both these areas contain 'vocabularies' of potential actions that are addressed either by external stimuli or internally, as for example during reaching or grasping movements executed in the dark. The difference between the two areas consists basically in their motor 'vocabularies': in F5 grasping movements related to the object intrinsic characteristics, in F4 reaching movements related to object spatial localization.

The possibility for the nervous system to internally represent an action in the absence of any motor contingency opens new exciting possibilities also for the interpretation of some perceptual mechanisms. The mirror neurons observation/execution matching system could be at the basis of inter-individual gestural communication (Rizzolatti et al., 1996) and, possibly, of the linguistic function (see Rizzolatti and Arbib, 1998). Visuomotor responses of F5 'canonical' neurons could play a role in object semantic categorization (see Rizzolatti and Gallese, 1997). Although it is certainly true that semantic analysis of objects involves temporal areas (pertaining to the so called 'ventral stream', see Ungerleider and Mishkin, 1982), it is also very plausible that a complete knowledge of objects semantics cannot exclude information on how to act on them. The concept of shape, for instance, is represented in a multiplicity of areas: shape is a geometrical property but also requires a motor knowledge (and a motor experience, possibly acquired during development) to be fully defined. Some recent neuropsychological data are in agreement with this view (Craighero et al., in press). Normal human subjects were required to prepare a grasping movement of a bar after the presentation of a visual stimulus whose orientation was either congruent or incongruent with that of the bar. The results showed that grasping preparation enhances the detection and discrimination of visual stimuli whose intrinsic properties are congruent with those of the object to be grasped. These results can be explained only by postulating a 'backward' influence that motor system exerts on areas traditionally considered as involved in sensory analysis of object characteristics.

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