



New insights on sensorimotor integration: From hand action to speech perception

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Abstract

In the last two decades the integrative role of the frontal premotor cortex (a mosaic of agranular/disgranular areas lying in front of the primary motor cortex) have been more and more elucidated. Among its various functions, sensorimotor transformation, and action representation storage, also for nonstrictly motor purposes, are the most intriguing properties of this region, as shown by several researches. In this article we will mainly focus on the ventro-rostral part of the monkey premotor cortex (area F5) in which visual information describing objects and others' acting hands are associated with goal-directed motor representations of hand movements. We will describe the main characteristics of F5 premotor neurons and we will provide evidence in favor of a parallelism between monkeys and humans on the basis of new experimental observations. Finally, we will present some data indicating that, both in humans and in monkeys, action-related sensorimotor transformations are not restricted to visual information but concern also acoustic information.

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1. Introduction

The capacity to use the hand for grasping objects represents an evolutionary new ability that characterizes the behavior of higher primates. The “precision grip,” characterized by the opposition of the index finger and the thumb in order to grasp and manipulate small objects, represents the zenith of such an ability. The kinematic analysis of grasping movements shows that the finger configuration present when the hand makes contact with an object, is the final outcome of a complex motor sequence starting at the beginning of the reaching–grasping movement (Jeannerod, 1988). As soon as the arm begins to move toward the object, the fingers start assuming the configuration necessary for grasping it (preshaping). The maximal aperture of the hand, although larger than that necessary for grasping the object, has a fixed relation with the size of the object. It is evident from this description that there are two fundamental requisites which are necessary for an effective

execution of grasping movements: (i) the capacity to transform the intrinsic visual properties of the object (shape and size) into finger movements and (ii) the capacity to fractionate and independently control finger movements.

Lesion experiments in monkeys and clinical data in humans show that a correct execution of grasping movements requires the integrity of area F1 (primary motor cortex or Brodmann area 4). Lesions of this area cause a profound deficit in what is a fundamental property of F1—the control of individual finger movements. As a consequence, individuals with F1 lesions are almost totally unable to grasp objects. The anatomical correlate of finger control is represented by the direct connections that F1 has with individual spinal motoneurons. As a result of this arrangement, F1 is able to overcome the reflex synergies and to recruit spinal cord motoneurons in variable combinations according to the size and shape of the object to be grasped. By injecting neural tracers into the hand field of F1, connections have been found with several frontal premotor areas. Among these areas, area F5 receives the largest amount of object-related visual information from the parietal

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lobe. Physiological studies confirmed that F5 plays a crucial role in the organization of grasping movements (see Jeannerod, Arbib, Rizzolatti, & Sakata, 1995).

Area F5 forms the rostral part of inferior area 6 (Fig. 1).

Microstimulation and single neuron studies show that in area F5 are represented hand and mouth movements. The two representations tend to be spatially segregated with hand movements mostly represented in the dorsal part of F5, whereas mouth movements are mostly located in its ventral part. Although not much is known about the functional properties of “mouth” neurons, the properties of “hand” neurons have been extensively investigated. Rizzolatti et al. (1988) recorded single neuron activity in monkeys trained to grasp objects of different size and shape. They found that most of the hand neurons discharge in association with goal-directed actions such as grasping, manipulating, tearing, and holding. F5 neurons do not discharge during finger and hand movements similar to those effective in triggering them when made with other purposes (e.g., scratching, pushing away). Furthermore, many F5 neurons become active during movements that have an identical goal regardless of the effectors used for attaining it. For example, many grasping neurons discharge when the monkey grasps an object with its right hand, with its left hand or with its mouth.

The class of neurons most represented in F5 is that of grasping neurons. Typically, these neurons begin to discharge before the contact between the hand and the object: Some of them stop firing immediately after contact, whereas others keep firing for a while after it. The temporal relation between grasping movement and neuron discharge varies from neuron to neuron. Some neurons become active during the initial phase of the movement (opening of the hand), some discharge during

hand closure, and others discharge during the entire grasping movement from the beginning of fingers opening until their contact with the object. In addition to temporal specificity, many grasping neurons discharge in association with a particular type of grip. Most of them are selective for one of the three most common monkey’s grip types: precision grip, finger prehension, and whole hand grasping. Sometimes there is also specificity within the same general type of grip. For instance, within the whole hand grasping, the prehension of a sphere, which requires the opposition of all fingers, is codified by different neurons from those codifying the prehension of a cylinder. A typical example of a grasping neuron is shown in Fig. 2. This neuron fires during precision grip (Fig. 2, top) but not during whole grasping (Fig. 2, bottom). Note that the neuron discharges both when the animal grasps with its right hand and when the animal grasps with its left hand.

Taken together, these data show that in area F5 there is a storage—a “vocabulary”—of motor actions related to the hand use. The “words” of the vocabulary are represented by populations of neurons. Each indicates a particular motor action or an aspect of it. Some indicate a complete action in general terms (e.g., take, hold, and tear). Others specify how objects must be grasped, held or torn (e.g., precision grip, finger prehension, and whole hand prehension). Finally, some subdivide the action in smaller segments (e.g., fingers flexion or extension).

2. Canonical and mirror “visuomotor responses” in monkeys

One of the most fascinating neurophysiological discoveries of the last two decades is that some *premotor neurons in addition to their motor discharge, respond also to the presentation of visual stimuli*. Neurons with this property mainly pertain to Frontal Eye Fields (FEF, Bruce & Golberg, 1985), to area F4 and to area F5 (Gentilucci, Scandolara, Pigarev, & Rizzolatti, 1983, 1988; Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981, 1988) that, taken together, represent the main target for the inferior parietal lobule projections carrying out visual information. Note that visual responses are related to the effectors that are somatotopically represented in these areas.

Let us examine the visuomotor responses of area F5. The motor properties of F5 described in Section 1 are common to all F5 neurons. If one examines, however, F5 neurons that respond also to visual stimuli, it becomes clear that in this area 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 et al., 1988; Rizzolatti & Fadiga, 1998). Neurons of the

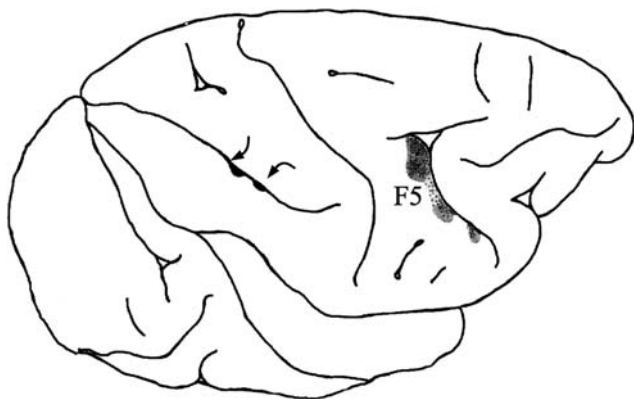


Fig. 1. Lateral view of monkey right hemisphere. Area F5 is buried inside the arcuate sulcus (posterior bank) and emerges on the convexity immediately posterior to it. Area F5 is bidirectionally connected with the inferior parietal lobule. Here, the F5 neurons labeled after two tracer injections (see arrows) in the anterior intraparietal area, are shown.

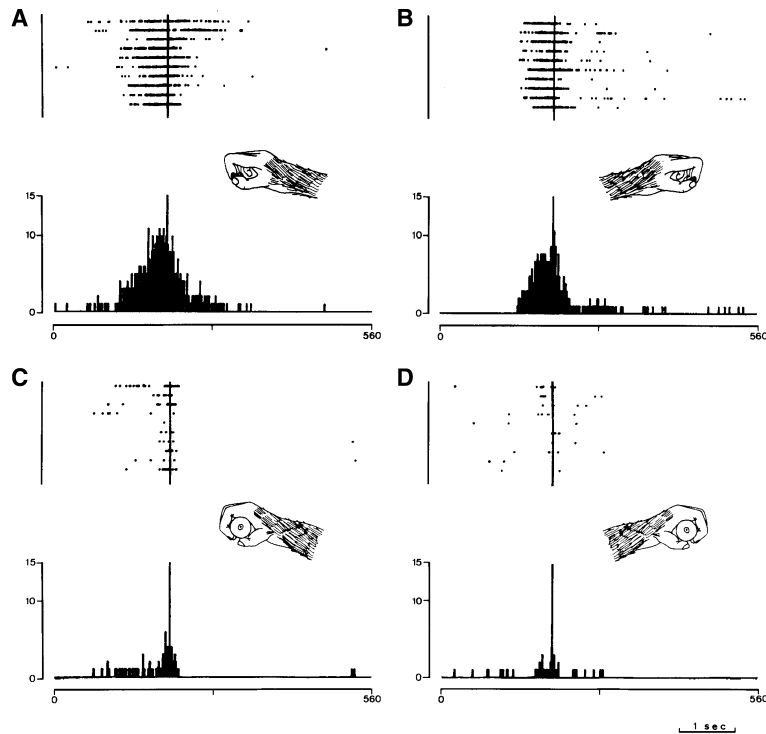


Fig. 2. A typical F5 grasping motor neuron. In the uppermost part of each panel eight successive trials are represented (rasters). Each dot represent an action potential. In the lowermost part the sum histogram is drawn. Trials are aligned with the moment at which the monkey touches the target (vertical lines across rasters and histograms). Ordinates: spikes/second; abscissae: 20 ms bins.

second category discharge when the monkey observes another individual making an action in front of it (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996a). For this peculiar “resonant” properties, neurons belonging to the second category have been named “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.

Recently, the visual responses of F5 “canonical” neurons have been re-examined using a formal behavioral paradigm, which allowed to separately test the response related to object observation, 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 3D graspable object. Among these visuomotor neurons, two thirds were selective to one or few specific objects.

Fig. 3A (grasping in light) shows the responses of a F5 visually selective neuron. While observation and grasping of a ring produced strong responses, responses to the other objects were modest (sphere) or virtually absent. Fig. 3B (object fixation) 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 task represented in A, 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 small size objects, discharge also during precision grip. On the contrary, neurons selectively active when the monkey looks at a large object, discharge also during actions directed towards large objects (e.g., whole hand prehension).

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

The visual stimuli most effective in triggering mirror neurons discharge are actions in which the experimenter’s

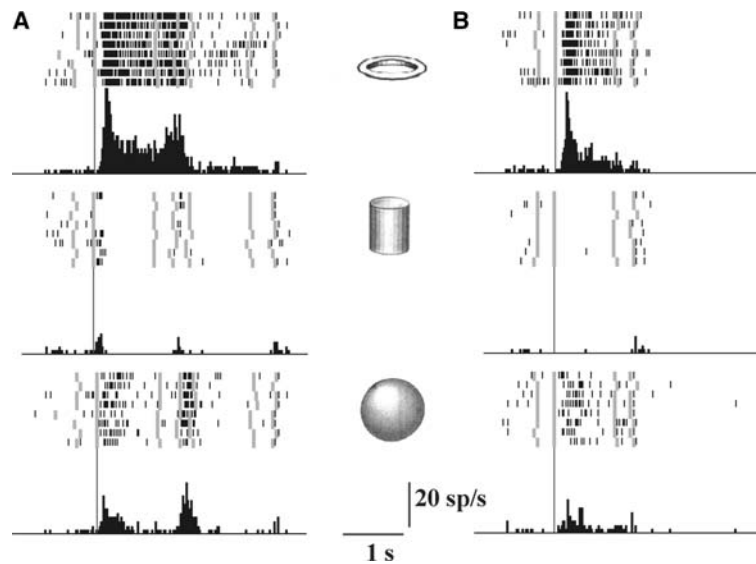


Fig. 3. Responses of a visuomotor neuron of the F5 area. Each panel shows the neuronal activity recorded during the observation and grasping (A) or the mere observation (B) of different 3D objects. The alignment of the single trials coincides with the moment in which the object becomes visible (line through rasters and histogram). In A, the first gray bar following the alignment represents the appearance of the signal which commands the beginning of grasping movement. The conventions used in the visualization of the responses are the same as those used in Fig. 2. Modified from Murata et al. (1997).

hand or mouth interacts with objects. The mere presentation of 3D objects or food is ineffective in evoking mirror neurons discharge. Similarly, actions made by 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, for example, during observation of grasping movements, but only when the object is grasped with the index finger and the thumb.

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). One representative highly congruent mirror neuron is shown in Fig. 4.

It is interesting to note that both canonical and mirror neurons are characterized by congruence between the action they motorically code and the observed-object/observed-action that evokes the visual discharge.

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 3D

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. 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 evokes 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 response 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 “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 characterizes mirror neurons could be at the basis of action imitation and action understanding (see Fadiga & Gallese, 1997; Rizzolatti et al., 1996b).

3. Canonical and mirror “visuomotor responses” in humans

Recently, a series of studies have addressed the question if visuomotor responses, similar to those

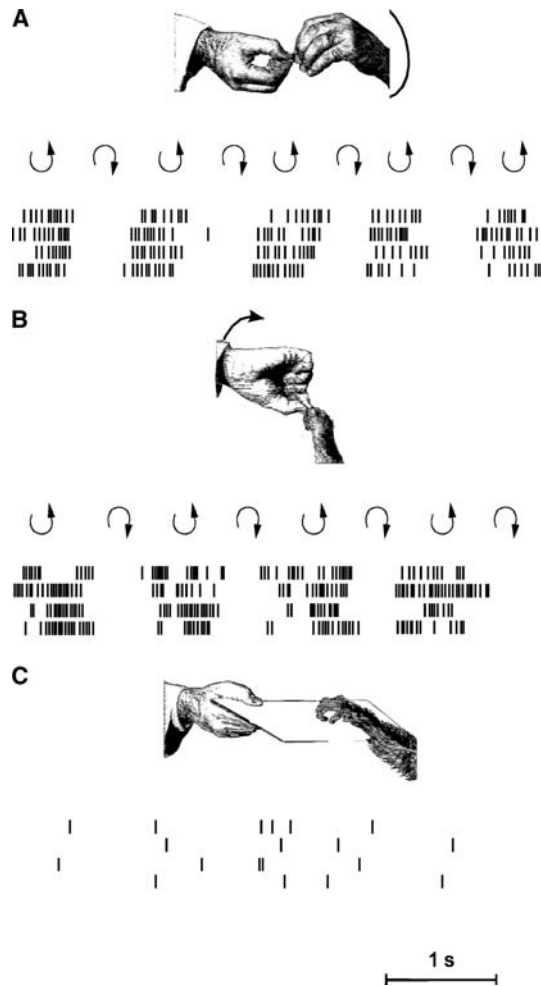


Fig. 4. Example of a highly congruent mirror neuron. The behavioral situations are schematically represented in the upper part of each panel. In the lower part are shown a series of consecutive rasters and the relative peristimulus response histograms. (A) The monkey observes the experimenter who rotates 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. From Rizzolatti et al. (1996).

observed in the monkey, are present also in humans. Thus, by approaching the theme with different techniques, these studies were aiming to establish the existence of a link between motor representation and both object-observation and action-observation.

3.1. Object-observation related responses

Evidence that an automatic link between objects and motor programs exists also in humans was recently provided by reaction time experiments carried out in normal subjects (Craighero, Fadiga, Umiltà, & Rizzol-

atti, 1996, 1998). In these experiments, drawings of differently oriented rectangles were presented on a computer screen around a fixation point before (–100 ms), simultaneously with (0 ms) or after (+100 ms) a go-signal, which consisted in a change in color of the fixation point (see Fig. 5A). At the appearance of the go-signal, the subject had to respond, as fast as possible, by grasping an object whose orientation was either the same or different from that of the presented drawing. The results showed a difference in reaction times when the drawings were presented before the go-signal. Reaction times decreased when the orientation of the drawing was the same of the orientation of the object to be grasped (congruent trials) (See Fig. 5B).

This facilitatory effect of congruent stimuli was present only when the drawing was presented before the go-signal. Note that, being the response exclusively determined by the go-signal, the analysis of the drawing has no utility for task solution. The effect of the congruent stimulus indicates, therefore, that the mere observation of a task-irrelevant visual stimulus automatically facilitates the grasping of a real object when the intrinsic properties of the latter are congruent with those of the drawing.

Another evidence that the presentation of an object may automatically facilitate actions directed to it, is given by a study of Tucker and Ellis (1998). These authors presented normal human subjects with photographs of common graspable objects. The subjects had to decide by a key-pressing made either with the left or the right hand whether the presented object was upright or inverted. The results showed that the reaction times were faster when the key-press response was executed by the hand most suited to grasp the presented object, suggesting that visual objects potentiate actions that may be performed on them, even in the absence of explicit intentions to act.

Direct evidence of an activation of premotor areas during observation of graspable objects was provided by a PET experiment (Grafton, Fadiga, Arbib, & Rizzolatti, 1997). Normal right-handed subjects were scanned during observation of bidimensional colored pictures (meaningless fractals), during observation of 3D objects (real tools attached to a panel), and during silent naming of the presented tools and of their use. The most important result was that the premotor cortex became active during the simple observation of the tools. This premotor activation was further augmented when the subjects named the tool use. This result shows that, as in the case of canonical F5 monkey neurons, also in the absence of any overt motor response or instruction to use the observed stimuli, the presentation of graspable objects increases automatically the activity of premotor areas.

A very recent PET study made by Grèzes and Decety (2002) indicated that the perception of objects,

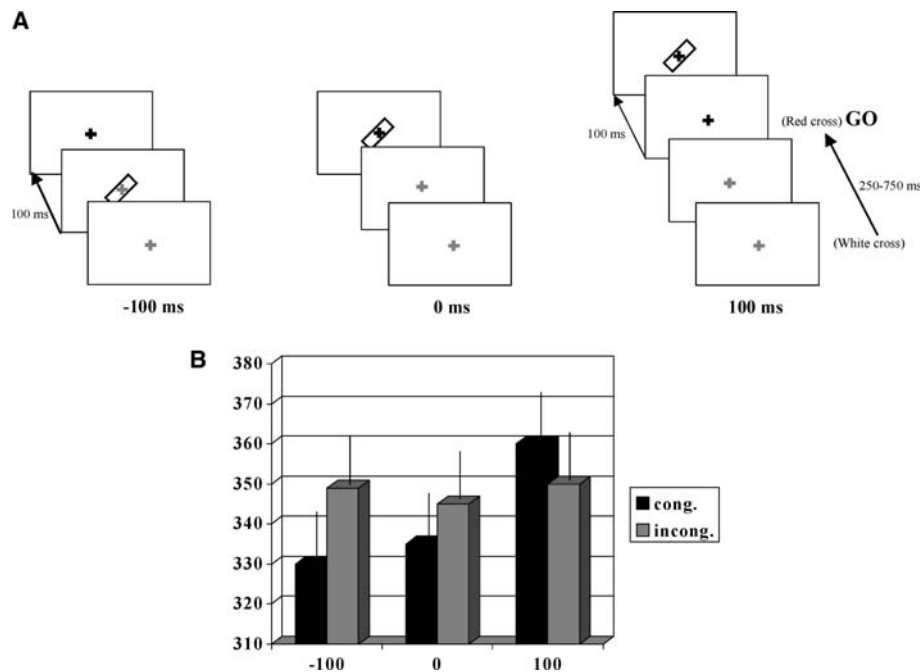


Fig. 5. (A) Schematic representation of the procedure used by Craighero et al. (1998). The beginning of the trial was marked by the appearance of the white (here gray) cross on the screen. After a variable interval (250–750 ms), the cross turned red (here black), giving the signal to execute the grasping response. Before (Stimulus Onset Asynchrony, SOA = -100 ms), simultaneously with (SOA = 0 ms) or after (SOA = 100 ms) the go-signal, drawings representing differently oriented rectangles were presented around the cross. (B) Mean RTs for congruent (cong.) and incongruent (incong.) trials in the three experimental conditions. Standard errors are represented by solid lines above each bar.

irrespective of the task required to the subject (judgement of the vertical orientation, motor imagery, and silent generation of the noun or of the corresponding action verb), versus perception of non-objects, was associated with activation of a common set of cortical regions. The occipito-temporal junction, the inferior parietal lobule, the SMA-proper, the pars triangularis in the inferior frontal gyrus, the dorsal and ventral precentral gyrus were engaged in the left hemisphere. The ipsilateral cerebellum was also involved. These activations are congruent with the idea of an involvement of motor representation already during the perception of objects, providing evidence that the perception of objects automatically affords actions that can be made toward them.

The monkey experiments reviewed above indicate that the presentation of graspable objects determines the automatic activation of the premotor area F5. From monkey neurophysiological studies it is known that the main origin of object-related visual information is a parietal area buried inside the intraparietal sulcus (area AIP, Sakata, Taira, Murata, & Mine, 1995). Given the fact that, in general, cortico-cortical connections are bidirectional, it is possible that the preparation to act toward an object facilitates the connected parietal areas rendering them more sensitive to detect the object toward which the action has been prepared. More in general, this putative mechanism could represent a way through which “intention to do” can influence perception.

The possibility of such a top-down activation was recently investigated by Craighero, Fadiga, Rizzolatti, and Umiltà (1999). The experiments were carried out in normal subjects instructed to grasp a bar (placed out of their sight) that could be oriented either clockwise or counterclockwise. Before the beginning of each trial the subjects were informed about the incoming bar orientation. The instructions were to prepare the required grasping movement and to execute it, as fast as possible, at the presentation of a go-signal. The go-signal consisted of a rectangle which was presented on the computer screen, around a fixation point. The orientation of the rectangle could be either the same or different as that of the bar. The results showed that reaction times to initiate grasping were faster in response to the rectangles whose orientation was the same of the bar to be grasped than to the rectangles having an opposite orientation. These data indicated that preparation of a specifically oriented grasping movement facilitates visual processing of stimuli sharing the same intrinsic properties.

3.2. Action-observation related responses

The first evidence of the existence of mirror-like visuo-motor activation in humans has been provided by Fadiga, Fogassi, Pavesi, and Rizzolatti (1995) in a transcranial magnetic stimulation (TMS) experiment. The motor cortex of normal human participants was

magnetically stimulated and motor evoked potentials (MEPs) were recorded from intrinsic and extrinsic hand muscles. It was reasoned that, if the observation of a hand movement activates the premotor cortex, this should, in turn, induce an enhancement of MEPs elicited by the magnetic stimulation of the hand representation of the motor cortex. The results confirmed this hypothesis showing a pattern of muscle facilitation revealed by TMS during action observation strictly resembling that occurring during actual execution of the observed movements. In other terms, looking at a hand closing onto an object evokes a facilitation of the observer's flexors muscles. Further experiments demonstrated the cortical origin of this facilitation (Baldissera, Cavallari, Craighero, & Fadiga, 2001; Strafella & Paus, 2000). Strafella and Paus (2000), by using the double stimulus TMS technique, showed that the interstimulus interval (I_t) between two close stimulations that evoked the larger motor facilitation during action viewing, was compatible with cortico–cortical facilitating connections. Baldissera et al. (2001) investigated the spinal excitability of hand motoneurons in normal volunteers while observing a video-clip showing different kinds of goal directed hand actions. Their results showed that, during observation of hand actions, the spinal excit-

ability was modulated *reciprocally* with respect to the effect shown by Fadiga et al. (1995) during cortical stimulation: when subjects were observing finger closing onto an object, hand flexors were inhibited while when a hand opening movement was shown, hand flexors muscles were facilitated. The opposite behavior was demonstrated for extensor muscles.

These experiments, taken together, indicate that during action observation there is both an activation of cortical areas connected (directly and/or indirectly) with M1 and the generation, in the spinal cord, of a signal opposite in sign that determines the reciprocal behavior observed by Baldissera et al. (2001) (see Fig. 6 for a schematic view of the proposed mechanism).

Note that the presence of such a peripheral, *movement-specific* inhibition may favour the cortical processing of observed actions, leaving free the cortical motor system to “re-act” the observed actions without the risk of overt movements generation. This “motorically silent” mapping of observed actions on the observer's motor repertoire might be at the basis of the identification/recognition process of actions performed by other individuals.

Further evidence that cortical motor areas are activated during movement observation comes from MEG

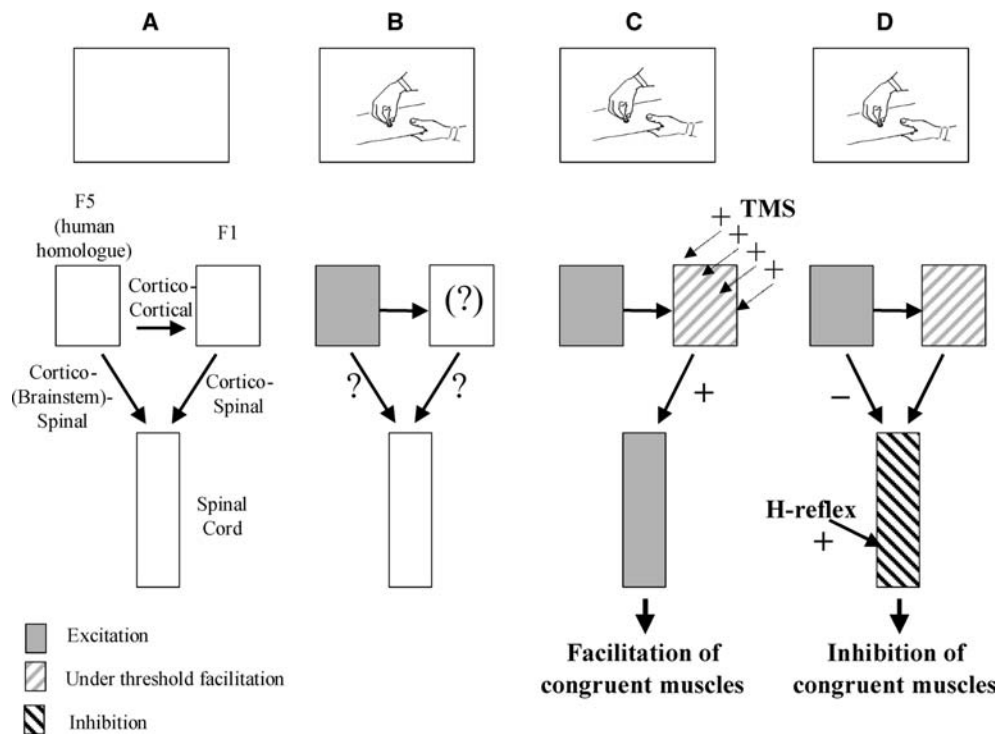


Fig. 6. Effects of action viewing at the cortical and spinal cord levels. (A) Schematic representation of the nervous centers and connections postulated to be involved during action observation. During hand action viewing (B), the human homologue of monkey's area F5 becomes active (mirror neurons, gray). Due to cortico–cortical connections linking F5 with primary motor cortex (F1), the excitation spreads to the primary motor cortex and facilitates it under threshold (diagonal gray bars) (C). We say ‘under threshold’ because: (1) normally, we do not move when we look at others’ actions; (2) single neuron recordings performed in monkey's area F1 never showed activation related to action observation (L.F., personal observation). When TMS is applied on F1 it reveals the underlying facilitation by inducing in hand muscles motor evoked potentials larger than those evoked during control conditions (C). When spinal excitability is tested with H-reflex technique, the reciprocal behavior is shown (D).

experiments. Hari et al. (1998) recorded neuromagnetic oscillatory activity of the human precentral cortex elicited by median nerve stimulation in healthy volunteers during rest (i), manipulation of a small object kept in their right hand (ii), and observation of another individual performing the same task (iii). The cortical 15–25 Hz rhythmical activity was measured. In agreement with previous data (Salmelin & Hari, 1994), this activity was suppressed during movement execution. Most interestingly, the rhythm was also significantly diminished during movement observation. Control experiments confirmed the specificity of the suppression effect. Because the recorded 15–25 Hz activity originates mostly in the anterior bank of the central sulcus, it appears that the human primary motor cortex desynchronizes (and therefore becomes more active) during movement observation in the absence of any active movement. Similar results were obtained also by Cochin, Barthelemy, Lejeune, Roux, and Martineau (1998), who recorded EEG from subjects observing video movies in which human movements were displayed. As a control, moving objects, moving animals, and still objects were presented. The data showed that the observation of human movements, but not that of objects or animals, desynchronizes the EEG pattern of the precentral cortex.

Recently, a series of reaction time experiments investigated the possibility that the activation of the premotor cortex induced by hand action preparation facilitates the discrimination of hand poses visually presented (Craighero, Bello, Fadiga, & Rizzolatti, 2002). Normal participants were instructed to prepare a hand grasping movement towards one of two bars that differed in orientation (clockwise or counterclockwise). They then had to execute the prepared grasping movement at the presentation of a picture representing a given hand pose (go-signal) on the computer screen. Two were the possible picture presented to subjects and both of them were images of the right hand as seen in a mirror. One represented the posture of the hand when it reached the bar clockwise oriented, the other represented the posture of the hand when it reached the bar counterclockwise oriented. At the presentation of the go-signal the subject had to respond by grasping the bar. The combination of picture and actual grasping gave origin to congruent and incongruent conditions. Results showed that the reaction times were faster when there was congruency between the hand depicted in the visual stimulus and the subsequent grip. A possible interpretation of this finding is the presence of a specific visuo-motor link between the visual stimulus and the subsequent action.

Which are the brain areas involved in the action-observation/execution resonant system? A series of brain imaging experiments were made in order to assess which cortical area could be the homologue of the monkey F5 mirror system. Hand grasping movements (Grafton,

Arbib, Fadiga, & Rizzolatti, 1996; Rizzolatti et al., 1996b) as well as, more recently, more complex hand/arm movements were used as visual stimuli (Decety et al., 1997; Grèzes, Costes, & Decety, 1998). The results of the first experiments showed that during the observation of hand grasping there was an activation of the left inferior frontal cortex, in correspondence of the Broca's region. In addition activations were found in the left superior temporal sulcus (STS), the rostral part of the left inferior parietal lobule (area 40), the left opercular parietal region and the rostral part of the supplementary motor area (SMA-proper) (Grafton et al., 1996; Rizzolatti et al., 1996b). The first three regions most likely correspond to the monkey cortical areas where there are neurons that discharge when the monkey observes biological actions, namely: area F5 (Gallese et al., 1996), the STS region (Carey, Perrett, & Oram, 1997; Perrett et al., 1989), and the rostral part of the inferior parietal lobule (Fogassi, Gallese, Fadiga, & Rizzolatti, 1998). In studies carried out by the Lyon group (Decety et al., 1997; Grèzes et al., 1998) the involvement of Broca's area during observation of hand/arm actions was further confirmed. The authors instructed subjects to observe meaningful (with a goal) and meaningless movements. The main results of the condition in which subjects observed meaningless arm movements were an activation of the parietal lobe bilaterally, in the left precentral gyrus and the cerebellum on the right side (Grèzes et al., 1998). On the contrary, the observation of meaningful hand actions, in addition to the already mentioned frontal and parietal areas, activates the left inferior frontal gyrus (Broca's region). Note that the activation of Broca's region during observation of action, suggests for this area the putative role of human homologue of area F5. In this direction point also some comparative cytoarchitectonical data (see Petrides & Pandya, 1994) and recent fMRI data from (Binkofski et al., 1999) demonstrating that Broca's region becomes active also during manipulation of complex objects. In a very recent fMRI study (Buccino et al., 2001) the authors were aiming to assess whether the observation of actions made with different effectors would activate specific parts of the premotor cortex in accord with the somatotopic organization of the region. While being scanned, normal participants were asked to carefully observe different videotaped object- and non-object-related actions, performed by another individual with different effectors (mouth, arm/hand, and foot). Results showed that observation of both object- and non-object-related actions determined a somatotopically organized activation of premotor cortex. The somatotopic pattern was similar to that of the classical motor cortex homunculus. In addition, during the observation of object-related actions, an activation, also somatotopically organized, was found in the posterior parietal lobe. Thus, when individuals observe an action, an

internal replica of that action is automatically generated in their premotor cortex. In the case of object-related actions, a further object-related analysis is performed in the parietal lobe, as if the subjects were indeed using those objects. These results bring the previous concept of an action observation/execution matching system (mirror system) into a broader perspective: this system is not restricted to the ventral premotor cortex, but involves several somatotopically organized motor circuits.

4. Is the visually evoked motor resonance the only example of motor activation induced in the brain by a sensory percept?

Both canonical and mirror F5 neurons discharge in response to visual stimuli. They address a common reservoir of action representation, that, in our view, could be used to categorize action-related visual percepts for imitation and identification purposes. Thus, in the case of canonical neurons, vision of graspable objects activates the motor representations more appropriate to interact with those objects; in the case of mirror neurons, objects alone are no more sufficient to evoke a premotor discharge: what is necessary is a visual stimulus describing a goal directed hand action in which both, an acting hand and a target must be present. Others' actions, however, do not generate only visually perceivable signals. Action-generated sounds and noises are also very common in nature. One could expect, therefore, that also these sensory information, related to a particular action, can determine a motor activation specific for that same action.

A very recent neurophysiological experiment addressed this point. Kohler et al. (2002) investigated whether there are neurons in area F5 that discharge when the monkey makes a specific hand action and also when it *hears* the corresponding action-related sounds, starting from the observation that a large number of object-related actions (e.g., breaking a peanut) can be recognized by a particular sound. The authors found that 13% of the investigated neurons discharge both when the monkey performed a hand action and when it heard the action-related sound. Moreover, most of these neurons discharge also when the monkey observed the same action demonstrating that these 'audio-visual mirror neurons' represent actions independently of whether they are *performed, heard* or *seen*.

These results have been very recently extended to humans by a TMS experiment (Fadiga, Craighero, Buccino, & Rizzolatti, 2002) during speech listening. In agreement with the idea originally proposed by Liberman (Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967; Liberman & Mattingly, 1985; Liberman & Wahlen, 2000), the authors started from the perspective that sounds conveying verbal communication

could be a vehicle of motor representations (articulatory gestures) shared by both the speaker and the listener, on which speech perception could be based upon. In other terms, the listener understands the speaker when his/her articulatory gestures representations are activated by verbal sounds (motor theory of speech perception). To test this hypothesis, normal subjects were requested to attend to an acoustically presented randomized sequence of disyllabic words, disyllabic pseudo-words and bitonal sounds of equivalent intensity and duration. Words and pseudo-words were selected according to a consonant–vowel–consonant–consonant–vowel (cvccv) scheme. The embedded consonants in the middle of words and of pseudo-words were either a double 'f' (labiodental fricative consonant that, when pronounced, requires slight tongue tip mobilization) or a double 'r' (lingua-palatal fricative consonant that, when pronounced, requires strong tongue tip mobilization). Bitonal sounds, lasting about the same time as verbal stimuli and replicating their intonation pattern, were used as a control. The excitability of motor cortex in correspondence of tongue movements representation was assessed by using single pulse transcranial magnetic stimulation (TMS) and by recording motor evoked potentials (MEPs) from the anterior tongue muscles. The TMS stimuli were applied synchronously with the double consonant of presented verbal stimuli (words and pseudo-words) and in the middle of the bitonal sounds. Results (see Fig. 7) showed that during speech listening there is an increase of motor evoked potentials recorded from the listeners' tongue muscles when the listened word strongly involves tongue movements, indicating that when an individual listens to verbal stimuli his/her speech related motor centers are specifically activated. Moreover, words-related facilitation was significantly larger than pseudo-words related one.

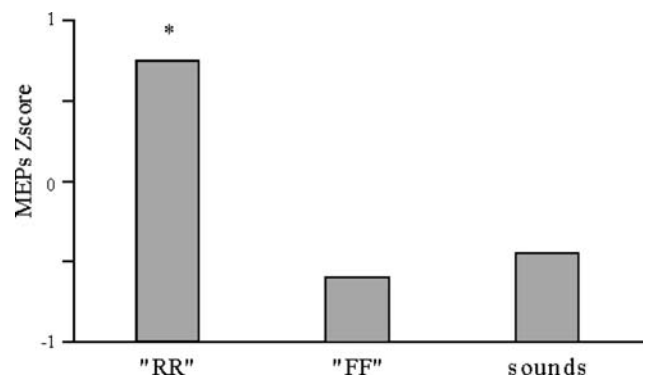


Fig. 7. Average value of intrasubject normalized MEPs total areas. "RR" and "FF" refer to verbal stimuli containing a double lingua-palatal fricative consonant "r," and containing a double labio-dental fricative consonant "f," respectively. The asterisk indicates that the MEPs z-score relative to the experimental condition "RR" is significantly higher than both those relative to the "FF" or the bitonal sounds presentation experimental conditions.

The presence of ‘audio-visual mirror neurons’ in the monkey and the presence of speech-related acoustic motor “resonance” in humans, indicate that independently from the sensory nature of the perceived stimulus, the mirror resonant system retrieves from action vocabulary (stored in the frontal cortex) the stimulus-related motor representations. The immediate translation of different sensory information into motor representations could be the key to have a congruent, unique representation of the environment, always crowded of acting individuals, allowing an automatic understanding of others’ different occupations.

5. Conclusions

The data reviewed in this paper altogether indicate that in both monkeys and humans there is a region of the premotor cortex that responds to actions-related sensory information. Experimental data suggest that in this premotor region action representations could be evoked by different types of sensory information: the mere vision of a sphere on a table, the vision of another individual’s hand reaching a cup, the sound of the breaking of a peanut and, in humans, also the sound of the voice of a friend calling us. When an action is evoked by visual or acoustic information this region “resonates” determining in the subject an internal, underthreshold for overt movement, activation mimicking the grasping of the sphere or of the cup, the breaking of the peanut, the articulation of the listened word. There are not yet enough experimental data to demonstrate the precise function of such a “mirror” system, even if its functional characteristics strongly suggest that it could be relevant for interindividual relationships (and imitation). What we know is that there is a brain region acting as a comparator between own and others’ motor representations that could allow individuals to “automatically understand” the perceived action just because they are able to reproduce, when necessary, that same action or, in other terms, the same sensory consequences of that action.

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