

CHAPTER 3

The mirror-neurons system: data and models

Laila Craighero¹, Giorgio Metta^{2,3}, Giulio Sandini^{2,3} and Luciano Fadiga^{1,3,*}

¹*D.S.B.T.A., Section of Human Physiology, University of Ferrara, Ferrara, Italy*

²*D.I.S.T., LiraLab, University of Genova, Genoa, Italy*

³*The Italian Institute of Technology, Morego, Genoa, Italy*

Abstract: In this chapter we discuss the mirror-neurons system, a cortical network of areas that enables individuals to understand the meaning of actions performed by others through the activation of internal representations, which motorically code for the observed actions. We review evidence indicating that this capability does not depend on the amount of visual stimulation relative to the observed action, or on the sensory modality specifically addressed (visual, acoustical). Any sensorial cue that can evoke the “idea” of a meaningful action activates the vocabulary of motor representations stored in the ventral premotor cortex and, in humans, especially in Broca’s area. This is true also for phonoarticulatory actions, which determine speech production. We present also a model of the mirror-neurons system and its partial implementation in a set of two experiments. The results, according to our model, show that motor information plays a significant role in the interpretation of actions and that a mirror-like representation can be developed autonomously as a result of the interaction between the individual and the environment.

Keywords: area f5; mirror-neurons system; canonical neurons; Broca’s area; action recognition; speech; single neuron recordings; transcranial magnetic stimulation; brain imaging

Introduction

Since our discovery of mirror neurons we suggested that they might have a role in action recognition and understanding (Di Pellegrino et al., 1992; Gallese et al., 1996; see Rizzolatti and Craighero, 2004). The core of this proposal is the following: when an individual acts, the motor consequences of her action are known by her brain. Mirror neurons allow this knowledge to be extended to actions performed by others. Every time an individual observes an action performed by another individual, neurons that represent that action are activated in the premotor cortex. The observer “understands” someone else’s actions

because the evoked motor representation corresponds to that generated internally during action execution (see Rizzolatti et al., 2001).

In order to better understand how this mechanism works it is necessary to clarify the functional properties of the monkey’s cortical region where mirror neurons have firstly been recorded (named F5 after Matelli et al., 1985).

Premotor mirror neurons: functional properties of monkey area F5

The monkey’s area F5 is a premotor area cytoarchitectonically non-homogeneous. Indeed, its part lying on the cortical convexity, that located in the caudal bank of the arcuate sulcus and

*Corresponding author. E-mail: fdl@unife.it

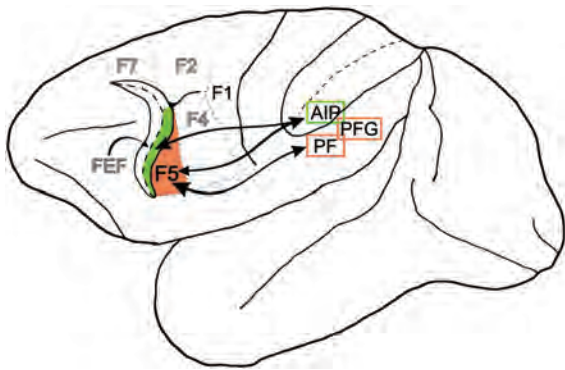


Fig. 1. Lateral view of monkey left hemisphere. Area F5 occupies the caudal bank of the arcuate sulcus (green) and the convexity immediately posterior to it (orange). Area F5 is bidirectionally connected with the inferior parietal lobule (areas AIP-anterior intra-parietal, PF and PFG). Within the frontal lobe, area F5 is connected with hand/mouth representations of primary motor cortex (area F1, labeled in bold in the figure).

that in the fundus of the arcuate sulcus — which defines the anterior border of area F5 — differ as far as cytoarchitectonics is concerned (Nelissen et al., 2005; Petrides, 2006). While the convexity and the caudal bank are mainly agranular, the fundus is dysgranular. The caudal bank and the convexity of area F5 differ also for their connections with the parietal lobe. While the bank is mainly connected with parietal area AIP (buried inside the intraparietal sulcus), the convexity is mainly connected with the exposed part of the inferior parietal lobule (areas PF and PFG of Barbas and Pandya, 1987; see Fig. 1).

Area F5 contains three types of neurons: motor neurons, “object observation-related” visuomotor neurons (also called canonical neurons), and “action observation-related” visuomotor neurons (mirror neurons). While motor neurons are distributed in the whole area, mirror neurons are mainly located in F5 convexity, and canonical neurons are mainly located in its bank.

Motor neurons

Motor neurons selectively discharge during execution of goal-directed hand/mouth actions (Rizzolatti et al., 1988). The specificity of the goal seems to be an essential prerequisite in activating

these neurons. The same neurons that discharge during grasping, holding, tearing, and manipulating are silent when the monkey performs actions that involve a similar muscular pattern but a different goal (e.g., grasping to put away, scratching, and grooming). Further evidence in favor of such a goal-directed representation is given by F5 neurons that discharge when the monkey grasps an object with either the right, the left hand or with the mouth. This observation suggests that some F5 premotor neurons can generalize the goal of the action, independently from the effector. F5 neurons can be sub-divided into several classes on the basis of the action that triggers the neural discharge. The most common types are “grasping,” “holding,” “tearing,” and “manipulating” neurons. Grasping neurons form the most represented class in area F5. Many of them are selective for a particular type of prehension such as precision grip, finger prehension, or whole-hand prehension. In addition, some neurons show specificity for different finger configurations, even within the same grip type. Thus, grasping a large spherical object (whole-hand prehension, requiring the opposition of all fingers) is coded by neurons different from those coding the prehension of a cylinder (also a type of whole-hand prehension but performed with the opposition of the four last fingers and the palm of the hand). Typically, F5 premotor 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 the contact. The temporal relation between grasping movement and neuron discharge varies from neuron to neuron. A group of 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 movement from the opening of the hand until their contact with the object. Taken together, the functional properties of motor F5 neurons suggest that this area stores a set of motor schemata (Arbib, 1997) or, as proposed earlier (Rizzolatti and Gentilucci, 1988), contains a “vocabulary” of motor acts. The “words” of this vocabulary are constituted by populations of neurons. Some of them indicate the general category of an action (hold, grasp, tear,

1 and manipulate), yet others specify the effectors
2 that are appropriate for that action. Finally, a
3 third group is concerned with the temporal seg-
4 mentation of the actions.

5 The motor vocabulary of actions of area F5 can
6 also be addressed without explicit action execu-
7 tion. Recent experiments have shown that several
8 F5 neurons discharge at the mere presentation of
9 objects whose shape and size is congruent with the
10 type of grip that is coded motorically by the same
11 neurons (object observation visuomotor neurons)
12 (Murata et al., 1997) or during observation of an-
13 other monkey or the experimenter making a goal-
14 directed action similar to that coded by the same
15 neurons (action observation visuomotor neurons)
16 (di Pellegrino et al., 1992; Gallese et al., 1996).

19 ***Object observation-related visuomotor neurons*** 20 ***(canonical neurons)***

21 Object observation visuomotor neurons are active
22 when manipulating an object and when fixating
23 the same object. These neurons discharge at the
24 mere presentation of objects whose shape and size
25 is congruent with the type of grasp coded motor-
26 ically by the same neurons.

27 The visual responses of object observation-re-
28 lated F5 neurons have been formally studied by
29 Murata and colleagues (Murata et al., 1997) using
30 a behavioral paradigm, which allowed to test sep-
31 arately the neurons' response to object observa-
32 tion, to the waiting phase between object
33 presentation and movements onset, and during
34 movement execution. The results showed that the
35 majority of these canonical visuomotor neurons
36 are selective to one or at most a few specific ob-
37 jects. Moreover, there is a strict congruence be-
38 tween their visual and motor properties: Neurons
39 that become active when the monkey observes
40 small objects discharge also during precision grip.
41 On the contrary, neurons selectively active when
42 the monkey looks at a large object discharge also
43 during actions directed toward large objects (e.g.,
44 whole-hand prehension). The most likely interpre-
45 tation for the visual discharge of these visuomotor
46 neurons is that there is a close link between the
47 most common three-dimensional stimuli and the

1 actions required to interact with them. Thus, every
2 time a graspable object is presented visually, the
3 corresponding F5 neurons are activated and the
4 action is "automatically" evoked. Under certain
5 circumstances this neural activity guides the execu-
6 tion of the movement directly; under others, it
7 remains an unexecuted representation of the ac-
8 tion that might be used for semantic knowledge.

11 ***Action observation-related visuomotor neurons*** 12 ***(mirror neurons)***

13 Action observation-related visuomotor neurons
14 are active when manipulating an object and when
15 watching someone else performing the same action
16 on the same object.

17 To be triggered by visual stimuli, action obser-
18 vation visuomotor neurons require an interaction
19 between a biologic effector (hand or mouth) and
20 an object. The sight of the object alone, that of an
21 agent mimicking an action, or an individual mak-
22 ing intransitive (non-object-directed) gestures are
23 all ineffective. The object significance for the mon-
24 key has no obvious influence on the mirror-neuron
25 response: Grasping a piece of food or a geometric
26 solid produces responses of the same intensity.

27 Mirror neurons show a large degree of general-
28 ization. Very different visual stimuli, but repre-
29 senting the same action, are equally effective. For
30 example, the same mirror neuron that responds to
31 a human hand grasping an object responds also
32 when the grasping hand is that of a monkey. Sim-
33 ilarly, the response is, typically, not affected if the
34 action is done near or far from the monkey, de-
35 spite the fact that the size of the observed hand is
36 obviously different in the two conditions. It is also
37 of little importance for neuron activation if the
38 observed action is eventually rewarded. The dis-
39 charge is of the same intensity if the experimenter
40 grasps the food and gives it to the recorded mon-
41 key or to another monkey introduced in the ex-
42 perimental room.

43 Typically, mirror neurons show congruence be-
44 tween the observed and executed action. This con-
45 gruence can be extremely faithful, i.e., the effective
46 motor action (e.g., precision grip) coincides with
47 the action that, when seen, triggers the neurons

(e.g., precision grip). For other neurons, the congruence is broader and the motor requirements (e.g., precision grip) are usually stricter than the visual ones (any type of hand grasping).

The most likely interpretation for visual discharge in mirror neurons is that it evokes an internal representation of the observed action. In other terms, the observed action selects, in the F5's motor vocabulary, a congruent "motor word," a potential action.

Actions do not generate only visual consequences and in fact action-generated sound and noise are also very common in nature. One could expect, therefore, that also this sensory information, related to a particular action, can determine a motor activation specific for that same action. Kohler et al. (2002) addressed this point by investigating F5 neurons that discharge when the monkey makes a specific hand action but also when it *hears* the corresponding action-related sounds. Auditory properties of the neurons were studied by using sounds produced by the experimenter's actions and non-action-related sounds. Neurons were not activated by non-action-related sounds, while they responded specifically to the sound of an object breaking and of paper ripping, which are the hand actions more frequently executed by the monkey. Neurons were studied in an experimental design in which two hand actions were randomly presented in vision-and-sound, sound-only, vision-only, and motor conditions (monkeys performing object-directed actions). The authors (Kohler et al., 2002) found that 13% of the investigated

neurons discharge both when the monkey performs a hand action and when it hears the action-related sound. Moreover, most of these neurons discharge also when the monkey observed the same action, demonstrating that these "audiovisual mirror neurons" represent actions independently of whether they are *performed, heard, or seen*.

A typical property of F5 mirror neurons is that their response is quite independent from the observer's point of sight. In other words, the same grasping action activates a given mirror neuron also if it is observed from different points of view (see Fig. 2).

How can the brain achieve an invariant description of a given action by using so different visual information? One possibility is that the system recognizes others' actions by using the same mechanisms it uses to visually control the execution of its own actions. In other terms, the point-of-view dependent visual information could be generalized by the invariance of the motor command driving action execution. To test this hypothesis, we manipulated the amount of visual information on the monkey own acting hand during grasping execution. Results showed that a significant percentage of F5 purely motor neurons are modulated by the vision of the own hand in action and that this modulation is mainly negative (less discharge) when the hand is not visible. These F5 (visuo)-motor neurons may have formed the original nucleus from which mirror neurons may have developed, possibly during the ontogenesis (Gesierich et al., in preparation). Figure 3 depicts a simplified

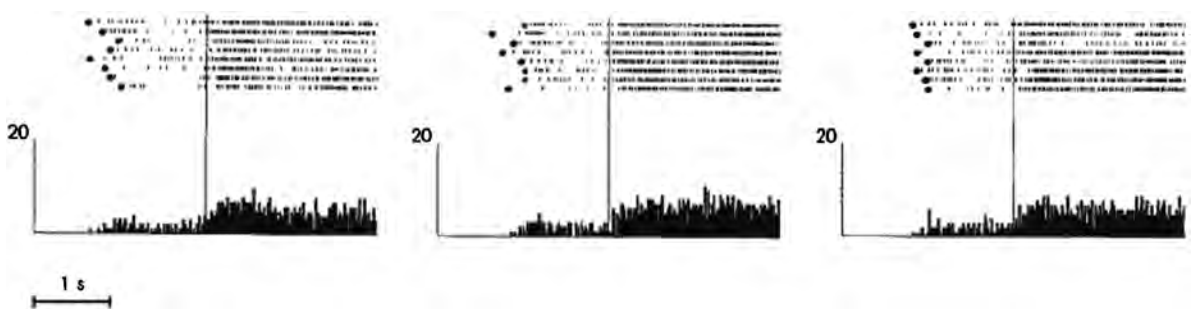


Fig. 2. A typical F5 mirror neuron discharging during the visual presentation of the same grasping movement, in the left visual hemifield (leftmost panel), centrally (central panel) or in the right visual hemifield (rightmost panel). Note the substantial equivalence of the responses. The vertical bars across rasters and histograms indicate the instant at which the experimenter touched the object. Ordinates, spikes per second. Histograms across bins, 20 ms. Adapted with permission from Gallese et al. (1996).

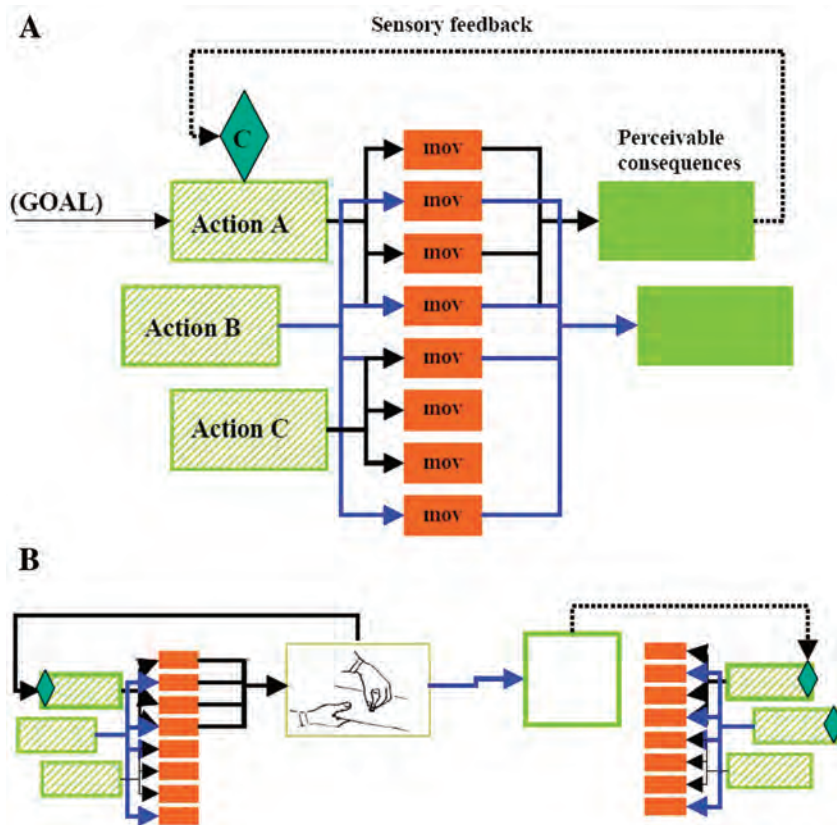


Fig. 3. (A) Simplified model of action representation. The actions level (area F5) is represented in the leftmost part of the figure. Action representations, if activated, activate in turn a set of motor synergies, here depicted in orange (mov, F1 level). Action execution does not produce consequences only on the external environment. Indeed, a series of afferent signals come back, from the periphery to the brain. These proprioceptive, visual, auditory signals (perceivable consequences, in the figure), are constantly monitored by the brain and used to control the development of the ongoing action, signaling also the goal achievement. The hypothesis we suggest is that proprioceptive and motor information, biologically invariant by definition during the actuation of a same motor command, are used by the brain to generalize (and to validate) the visual inputs related to the ongoing action. These visual inputs, that continuously vary depending on the position of the head with respect to the acting hand, are forcedly considered as homologs because they are generated by the same (or very similar) motor program. (B) Simplified model of action recognition. Two individual “brains” are shown, each one organized according to the scheme of A. When the individual on the left grasps an object her motor system receives a visual description of the ongoing movement that could be used to control its correct execution. At the same time, however, the observer’s “brain” on the left sees the same scene (with some changes of perspective). Due to the visuomotor coupling she created to control her own movements through the process previously described, this visual representation of the seen action gains the access to the correspondent motor representation (following the dotted line). This is, in our view, the “recognition” played by mirror neurons.

schema of this model, which will be more formally described in the last section of this chapter.

The mirror-neuron system and action recognition: prospective or reactive mechanisms?

The functional properties of F5 neurons indicate that in primates the action representations are addressed not only for motor execution, but also during observation of graspable objects, and perception (visual, acoustical, other?) of actions

performed by others. The presence of such a “vocabulary” of actions has important functional implications. Firstly, the execution of motor commands is strongly facilitated. The existence of preformed motor schemata, which are anatomically linked (hardwired) with cortical (primary motor cortex) and sub-cortical motor centers, facilitates the selection of the most appropriate combination of movements simply by addressing the general idea of an action. Thus, the number of variables that the motor system (at the premotor level) has to control to achieve the action goal is reduced. Secondly, it simplifies the association between a given stimulus (i.e., a visually presented object) and the appropriate motor response. This is the case of object observation-related visuomotor responses. Thirdly, it gives the brain a store of “ideas of action” that could be activated whenever visual or acoustic stimuli suggesting that another person is executing an action are perceived. This is the case of action perception-related sensorimotor responses.

On the basis of these functional properties that characterize not only mirror neurons but all the neurons in F5 region, it can be hypothesized that mirror neurons are at the basis of action recognition/understanding, and that this capability is not strictly dependent from the amount of stimulation perceived by the individual.

Evidence in monkeys

The hypothesis that complete visual information about the perceived action is not necessary to determine mirror neurons activation was directly tested by Umiltà and colleagues (Umiltà et al., 2001). The experimental paradigm consisted of two sessions. In the first session, the monkey was shown with a fully visible action directed toward an object or with the mimicry of the same action in the absence of the object. From previous studies it was known that mirror neurons do not discharge when the object is absent. In the second session, the monkey saw exactly the same experimental conditions but with the final part of the action hidden by a screen. Before each trial the experimenter could choose whether to place a piece of

food behind the screen so that also the monkey knew whether a target for the action was present. The main result of the experiment was that several neurons discharged in the “hidden” condition, but only when the animal knew that the food was present. This evidence was interpreted as a good demonstration that mirror neurons fire also during the reaching/grasping of an object placed out of sight, as long as the intention and the plausibility of the reaching/grasping action are clear.

The conclusion is that understanding of the action is not fully based on the visual description of the scene but it refers also to the motor representation of the action goal, shared by both the agent and the observer, and triggered by the context in which the action is performed (i.e., the presence or the absence of the food on the table behind the screen).

Evidence in humans

In recent years, a series of brain imaging studies demonstrated that a mirror-neuron system is also present in the human brain. When an individual observes an action, or executes it, a network of cortical areas is activated, including the ventral premotor cortex, the inferior frontal gyrus, the inferior parietal lobule and the superior temporal cortex (see for review Rizzolatti and Craighero, 2004). Furthermore, transcranial magnetic stimulation (TMS) was used to directly investigate the involvement of the motor system in humans during observation of others’ actions. TMS is an alternative technique to the single neuron recordings that can be used in humans to obtain good temporal resolution. Single or paired-pulse TMS allows to measure cortical excitability during different phases of an observed action. Moreover, this technique can help to verify the specific involvement of the motor system by discriminating the muscles that are involved in the motor replica. A series of TMS experiments showed that also in humans the mirror system is not strictly dependent on the visual stimulation but it is active whenever a motor representation is addressed (Gangitano et al., 2004; Borroni et al., 2005).

1 Gangitano and colleagues (Gangitano et al.,
2001) in a TMS experiment evoked motor-evoked
3 potentials (MEPs) in the first dorsal interosseus
4 muscle at different time intervals, while subjects
5 were watching a video clip of a hand approaching
6 and grasping a ball and demonstrated that the
7 specific activation of the observer's muscles is tem-
8 porally coupled to the dynamics of the observed
9 action. In a further experiment Gangitano et al.
10 (2004) investigated whether this pattern of modu-
11 lation was the consequence of a "resonant plan"
12 evoked at the beginning of the observation phase
13 or whether the plan was fractioned in different
14 phases sequentially recruited during the course of
15 the ongoing action. The authors therefore used the
16 same procedure as in Gangitano et al. (2001) with
17 the following exception: Subjects were shown
18 video clips representing an unnatural movement,
19 in which the temporal coupling between reaching
20 and grasping components was disrupted, either by
21 changing the time of appearance of maximal finger
22 aperture, or by substituting it with an unpredict-
23 able closure. In the first case, the observation of
24 the uncommon movements did not exert any modu-
25 lation in motor excitability. In the second case,
26 the modulation was limited to the first time of
27 stimulation. Modulation of motor excitability was
28 clearly suppressed by the appearance of the sudden
29 finger closure and was not substituted by any other
30 pattern of modulation. This finding suggests that a
31 motor plan, which includes the temporal features
32 of the natural movement, is activated immediately
33 after the observed movement onset and is dis-
34 carded when these features cease to match the vis-
35 ual properties of the observed movement. Thus,
36 the human mirror system seems to be able to infer
37 the goal and the probability of an action during
38 the development of its ongoing features.

39 Recently, Borroni et al. (2005) aimed at verify-
40 ing the degree of correspondence, especially with
41 respect to a fine temporal resolution, between the
42 observation of prolonged movements and its modu-
43 latory effects in the observer. For this purpose
44 the authors asked subjects to watch a cyclic flex-
45 ion-extension movement of the wrist. The same
46 sinusoidal function was used to fit both observed
47 wrist oscillation and motor resonance effects on
the observer's wrist motor circuits. In this way the

1 authors could describe a continuous time course of
2 the two events and precisely determine their phase
3 relation. MEPs were elicited in the right forearm
4 muscle of subjects who were observing a 1 Hz cy-
5 clic oscillation of the right hand executed by an-
6 other person. The results indicated that movement
7 observation elicited a parallel cyclic excitability
8 modulation of the observer's MEP responses fol-
9 lowing the same period as the observed movement.
10 Interestingly, the MEP modulation preceded the
11 observed movement, being related to time course
12 of muscular activation of the demonstrator and
13 not to the visually perceived movement. This find-
14 ing indicates that the mirror-neuron system antic-
15 ipates the movement execution, rather than simply
16 reacting to it.

17 Thus, the involvement of observer's motor sys-
18 tem is not necessarily consequent to the explicit
19 visual description of the complete action but,
20 rather, it may intervene in filling gaps because it
21 gives to the observer an implicit motor knowledge
22 about the observed action. In other words, the
23 mirror system seems to possess the capability to
24 predict the action outcome.

25 In this line are the data by Kilner and colleagues
26 (Kilner et al., 2004). In an event-related potentials
27 experiment, these authors showed that the readi-
28 ness potential (RP), a well-known electrophysio-
29 logical marker of motor preparation, is detectable
30 also during action observation. Furthermore,
31 when the upcoming action is predictable, the rise
32 of the RP precedes the observed movement onset.
33 They recorded electroencephalograms from sub-
34 jects while they watched a series of short video
35 clips showing an actor's right hand and a colored
36 object. In half of the videos the hand moved, while
37 in the other half it remained stationary. At the
38 beginning of each video the color of the object
39 indicated whether the hand would subsequently
40 move or not. Thus, the observed movements were
41 entirely predictable from the color of object in the
42 video. The results revealed a significant negative
43 gradient that started 500 ms before the onset of the
44 observed hand movement. This activity was com-
45 parable with the onset of the movement-related
46 RP produced when subjects actually executed a
47 movement. These results suggest an active role of
the mirror system in setting up an anticipatory

1 model of another person's action, endowing our
 3 brain with the ability to predict his or her inten-
 tions ahead of their realization.

5 All the reported experiments, however, investi-
 7 gated the involvement of the mirror system during
 observation of real hands executing goal directed
 9 actions. In a very recent experiment our group
 (Fadiga et al., 2006) wanted to verify if the vision
 of a real hand is a necessary prerequisite to activate
 the mirror system, or if any cue suggesting the
 11 presence of a hand performing meaningful move-
 ments is a sufficient stimulus. To this purpose we
 13 submitted human subjects to an fMRI scanning
 while they were observing a particular category of
 hand gestures: Hand shadows representing animals
 15 opening their mouths. Hand shadows only implicitly
 “contain” the hand creating them (i.e., hands are
 not visible but subjects are aware of the fact that
 the presented animals are produced by the hands).
 17 Therefore, they are interesting stimuli that might
 be used to answer the question of how much and
 what details of a hand gesture activate the mirror-
 neuron system. During the fMRI scan, healthy vol-
 19 unteers ($n = 10$) observed videos representing
 (i) the shadows of human hands depicting animals
 opening and closing their mouths, (ii) human
 hands executing sequences of meaningless finger
 23 movements, or (iii) real animals opening their
 mouths. Each condition was contrasted with a
 “static” condition, where the same stimuli pre-
 25 sented in the movie were shown as static pictures
 (e.g., stills of animals presented for the same
 amount of time as the corresponding videos). In
 addition, to emphasize the action component of
 the gesture, brain activations were further com-
 27 pared between pairs of conditions in a block de-
 sign.

37 Figure 4 shows, superimposed, the results of the
 39 moving vs. static contrasts for animal hand shad-
 ows and real animals conditions (red and green
 spots, respectively). In addition to largely over-
 41 lapping occipito-parietal activations, a specific dif-
 ferential activation emerged in the anterior part
 of the brain. Animal hand shadows strongly ac-
 43 tivated left parietal cortex, pre- and post-central
 gyri (bilaterally), and bilateral inferior frontal
 45 gyrus (BA 44 and 45). Conversely, the only
 frontal activation reaching significance in the
 47 moving vs.

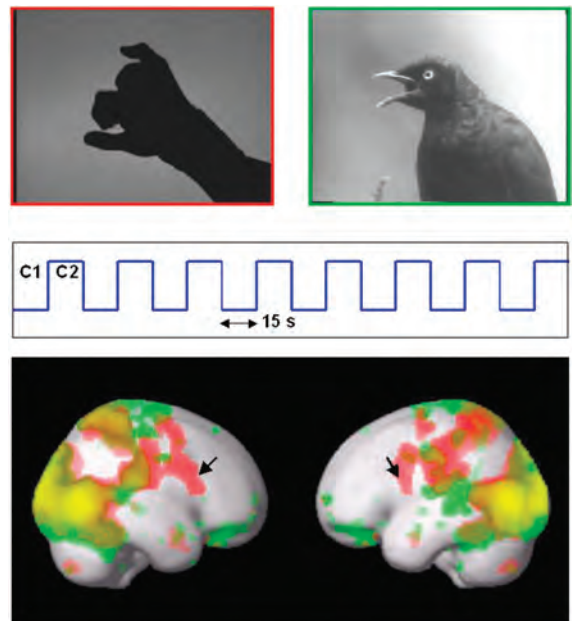


Fig. 4. Cortical activation pattern during observation of animal hand shadows and real animals. Significantly activated voxels ($P < 0.001$) in the moving animal shadows (red clusters) and moving real animals (green clusters) conditions after subtraction of the static controls. In the middle part of the figure, the experimental time-course for each contrast is shown (i.e., C1, moving; C2, static). Note the almost complete absence of frontal activation for real animals in comparison to animal shadows, which bilaterally activate the inferior frontal gyrus (arrows). Adapted with permission from Fadiga et al. (2006).

static contrast for real animals was located in bi-
 lateral BA 6, close to the premotor activation
 shown in an fMRI experiment by Buccino and
 colleagues (Buccino et al., 2004) where subjects
 observed mouth actions performed by monkeys
 and dogs. This location may therefore correspond
 to a premotor region where a mirror-neuron sys-
 tem for mouth actions is present in humans. The
 results shown in Fig. 4 indicate that the shadows
 of animals opening their mouths, although clearly
 depicting animals and not hands, convey implicit
 information about the human being moving her
 hand in creating them. Indeed, they evoke an ac-
 tivation pattern, which can be superimposed to
 that evoked by hand action observation (Grafton
 et al., 1996; Buccino et al., 2001; Grezes et al.,
 2003). Thus, the results demonstrate that the mir-
 ror-neuron system becomes active even if the

1 pictorial details of the moving hand are not explicitly visible: In the case of our stimuli, the brain
3 “sees” the performing hand also behind the visual
5 appearance. Consequently, the human mirror system (or at least part of it) can be seen more as an
7 active interpreter than as a passive perceiver (or resonator).

9 The possibility to be an active interpreter is based on the knowledge of the context in which the
11 observed action is performed. Different cues coming from the environment activate the representation
13 of the most probable action: in the Umiltà experiment (Umiltà et al., 2001) the knowledge of the presence of the food behind the screen gives
15 plausibility to the hidden action; in the Kilner experiment (Kilner et al., 2004) the color of the object at the beginning of the trial prompts the belief
17 that a grasping towards that object is going to be executed; in the Fadiga experiment (Fadiga et al., 2006) the old memory of playing with shadows on
19 the wall during childhood links the observed animal shadows with hand movements. Recently, we
21 tested the possibility that the mirror-neurons system could be modulated by the canonical neurons
23 activation determined by the vision of the to-be-grasped object (Craighero et al., in press). To this
25 purpose we asked subject to detect the instant at which the demonstrator’s hand touched the object.
27 Two different types of grasping on the same object were presented, differing for the type of fingers
29 opposition space: In one case the type of grasping was the one more commonly chosen to grasp the
31 presented object, in the other case it was a less appropriate one. This experimental manipulation
33 created a situation of conflict in terms of motor representations determining two main conditions:
35 A congruent one, in which the motor program evoked by object observation coincides with that
37 executed by the experimenter, and an incongruent one, where the two motor programs differ. Our
39 results showed that subjects’ response times are well below those commonly found in simple reaction
41 times tasks (usually around 120–150 ms), indicating that, to accomplish the task, subjects
43 indeed use a predictive model of the seen action. Moreover, response times were shorter for suitable
45 grasping trials than for not suitable ones. This indicates that action prediction is based on the

1 internal motor representation of the seen action, and that whenever incongruence is present between
3 the action evoked in the observer by the to-be-grasped object and the observed action, actually
5 executed on it, the ability to predict the action outcome decreases.

7 Considering both the functional properties of the neurons of the ventral premotor cortex of the
9 monkey and those of the human mirror-neurons system, as described by TMS and brain imaging
11 experiments, we can argue that the ventral premotor cortex is automatically activated whenever
13 the “idea” of an action is even suggested. This suggestion can derive from the sight of a graspable
15 object, as in the case of canonical neurons (Murata et al., 1997), from the visual (di Pellegrino et al.,
17 1992) or acoustical (Kohler et al., 2002) perception of a transitive action performed by another individual,
19 as in the case of mirror neurons in monkeys and of mirror-neurons system in humans (see Rizzolatti
21 and Craighero, 2004). Moreover, experimental evidence indicates that the idea of an action
23 does not necessarily require a complete perceptual stimulation to be elicited (Umiltà et al., 2001;
25 Fadiga et al., 2006).

27 In conclusion, the properties of the mirror-neurons system not only are in favor of its role in
29 action understanding, but clearly suggest that mirror neurons are fundamental in interpreting others’
31 intentions and in anticipating the outcome of others people’s actions, providing a key mechanism
33 to successfully interact in a social environment.

35 **Broca’s area is the core center of the human mirror-neurons system** 37

39 As discussed in the previous section, experimental evidence demonstrates that a mirror-neurons system
41 is also present in the human brain. The first evidence of the existence of a mirror-like visuo-
43 motor activation in the human brain has been provided by Fadiga et al. (1995) by a TMS experiment.
45 The motor cortex of normal human participants was magnetically stimulated and MEPs were recorded
47 from intrinsic and extrinsic hand muscles. It was reasoned that, if the observation of

1 a hand movement activates the premotor cortex,
 2 this should, in turn, induce an enhancement of
 3 MEPs elicited by the magnetic stimulation of the
 4 hand representation of the motor cortex. The re-
 5 sults confirmed this hypothesis showing a pattern
 6 of muscle facilitation during action observation
 7 that strictly resembles that occurring during the
 8 actual execution of the observed movements. In
 9 other words, looking at a hand closing onto an
 10 object evokes a facilitation of the observer's flexors
 11 muscles. Strafella and Paus (2000), by using the
 12 double stimulus TMS technique, demonstrated the
 13 cortical origin of this facilitation. They showed
 14 that the interstimulus interval between two close
 15 stimulations, which evoked the larger motor facil-
 16 itation during action observation, was compatible
 17 with cortico-cortical facilitating connections.

18 Further evidence that cortical motor areas are
 19 activated during movement observation comes
 20 from MEG experiments. Hari and colleagues
 21 (Hari et al., 1998) recorded neuromagnetic oscil-
 22 latory activity of the human precentral cortex elic-
 23 ited by median nerve stimulation in healthy
 24 volunteers during rest (i), manipulation of a small
 25 object with their right hand (ii), and observation of
 26 another individual performing the same task (iii).
 27 The cortical 15–25 Hz rhythmical activity was
 28 measured. In agreement with previous data (Sal-
 29 melin and Hari, 1994), this activity was suppressed
 30 during movement execution. Most interestingly,
 31 the rhythm was also significantly diminished dur-
 32 ing movement observation. Control experiments
 33 confirmed the specificity of the suppression effect.
 34 Because the recorded 15–25 Hz activity originates
 35 mostly in the anterior bank of the central sulcus, it
 36 appears that the human primary motor cortex de-
 37 synchronizes (and therefore becomes more active)
 38 during movement observation in the absence of
 39 any active movement. Similar results were ob-
 40 tained also by Cochin and colleagues (Cochin et
 41 al., 1998), who recorded EEG from subjects ob-
 42 serving videos where human movements were dis-
 43 played. As a control, moving objects, moving
 44 animals, and still objects were presented. The data
 45 showed that the observation of human move-
 46 ments, but not that of objects or animals, desyn-
 47 chronizes the EEG pattern of the precentral
 cortex.

1 A series of brain imaging experiments were car-
 2 ried out in order to assess which cortical area
 3 could be the homolog of the monkey F5 mirror
 4 system. Hand grasping movements (Grafton et al.,
 5 1996; Rizzolatti et al., 1996) as well as, more re-
 6 cently, more complex hand/arm movements were
 7 used as visual stimuli (Decety et al., 1997; Grezes
 8 et al., 1998). The results of the first experiments
 9 showed that during the observation of hand grasping,
 10 among the activation of other areas, there was
 11 an activation of the left inferior frontal cortex, in
 12 correspondence of the Broca's region, a region
 13 historically known to be involved in language pro-
 14 duction (Broca, 1861). In studies carried out by the
 15 Lyon group (Decety et al., 1997; Grezes et al.,
 16 1998) the involvement of Broca's area during ob-
 17 servation of hand/arm actions was further con-
 18 firmed. The authors instructed subjects to observe
 19 meaningful (with a goal) and meaningless move-
 20 ments. The main result when subjects observed
 21 meaningless arm movements was the bilateral ac-
 22 tivation of the parietal lobe, the activation of the
 23 left precentral gyrus and that of the right side of
 24 the cerebellum (Grezes et al., 1998). On the con-
 25 trary, the observation of meaningful hand actions,
 26 in addition to the already mentioned frontal and
 27 parietal areas, activated the left inferior frontal
 28 gyrus (Broca's region). More recently, two addi-
 29 tional studies have shown that a meaningful hand-
 30 object interaction, more than pure movement ob-
 31 servation, is effective in triggering Broca's area
 32 activation (Hamzei et al., 2003; Johnson-Frey et
 33 al., 2003). Similar conclusions have been reached
 34 also for the observation of mouth movements
 35 (Campbell et al., 2001). These results, together
 36 with comparative cytoarchitectonical data (see
 37 Petrides and Pandya, 1994; Nelissen et al., 2005;
 38 Petrides, 2006), and fMRI data from Binkofsky
 39 and colleagues (Binkofski et al., 1999) demon-
 40 strating that Broca's region becomes active also
 41 during manipulation of complex objects, suggest
 42 that Broca's region has the putative role of human
 43 homolog of area F5 in the monkey.

1 *Mirror-neurons system and speech recognition*

3 The presence of an audio-motor resonance (Kohler et al., 2002) in a region that, in humans, is classically considered a speech-related area, immediately evokes the Liberman's motor theory of speech perception (Liberman et al., 1967; Liberman and Mattingly, 1985; Liberman and Whalen, 2000). This theory maintains that the ultimate constituents of speech are not sounds but articulatory gestures that have evolved exclusively at the service of language. Consequently, speech perception and speech production processes can share a common repertoire of motor primitives that, during speech production, are at the basis of the generation of articulatory gestures, and during speech perception are activated in the listener as the result of an acoustically evoked motor "resonance." According to Liberman's theory, the listener understands the speaker when his/her articulatory gestural representations are activated by listening to verbal sounds. Although this theory is not unanimously accepted, it offers a plausible model of an action/perception cycle in the frame of speech processing.

7 To investigate if speech listening activates listener's motor representations, our group (Fadiga et al., 2002), in a TMS experiment, tested for the presence in humans of a system that motorically "resonates" when an individual listen to verbal stimuli. Healthy subjects were requested to attend to an acoustically presented randomized sequence of disyllabic words, disyllabic pseudowords and bitonal sounds of equivalent intensity and duration. Words and pseudowords were selected according to a consonant-vowel-consonant-consonant-vowel (cvccv) scheme. The embedded consonants in the middle of words and of pseudowords 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 the motor cortex in correspondence of the representation of tongue movements was assessed by

1 using single pulse TMS and by recording MEPs from the anterior tongue muscles. The TMS stimuli were applied synchronously with the double consonant of the presented verbal stimuli (words and pseudowords) and in the middle of the bitonal sounds. Results showed that during speech listening there is an increase of the MEPs recorded from the listeners' tongue muscles when the word strongly involves tongue movements. This indicates 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 pseudowords related one. These results indicate that the passive listening to words that would involve tongue mobilization (when pronounced) induces an automatic facilitation of the listener's motor cortex. Furthermore, the effect is stronger in the case of words than in the case of pseudowords suggesting a possible unspecific facilitation of the motor speech center due to recognition that the presented material belongs to an extant word.

23 Similar results were obtained by Watkins and colleagues (Watkins et al., 2003). By using TMS technique they recorded MEPs from a lip (*orbicularis oris*) and a hand muscle (first dorsal *interosseus*) in four conditions: listening to continuous prose, listening to non-verbal sounds, viewing speech-related lip movements, and viewing eye and brow movements. Compared to control conditions, listening to speech enhanced the MEPs recorded from the *orbicularis oris* muscle. This increase was observed only in response to the stimulation of the left hemisphere. No changes of the MEPs in any condition were observed following the stimulation of the right hemisphere. Finally, the size of MEPs elicited in the first *interosseus* muscle did not differ in any condition.

39 Taken together these experiments show that when an individual listen to verbal stimuli there is an activation of the speech-related motor centers. It is however unclear if this activation could be interpreted in terms of an involvement of motor representations in speech processing and, perhaps, in perception.

47 In order to investigate the perceptual role of Broca's area and considering that this area has been classically considered specifically involved in

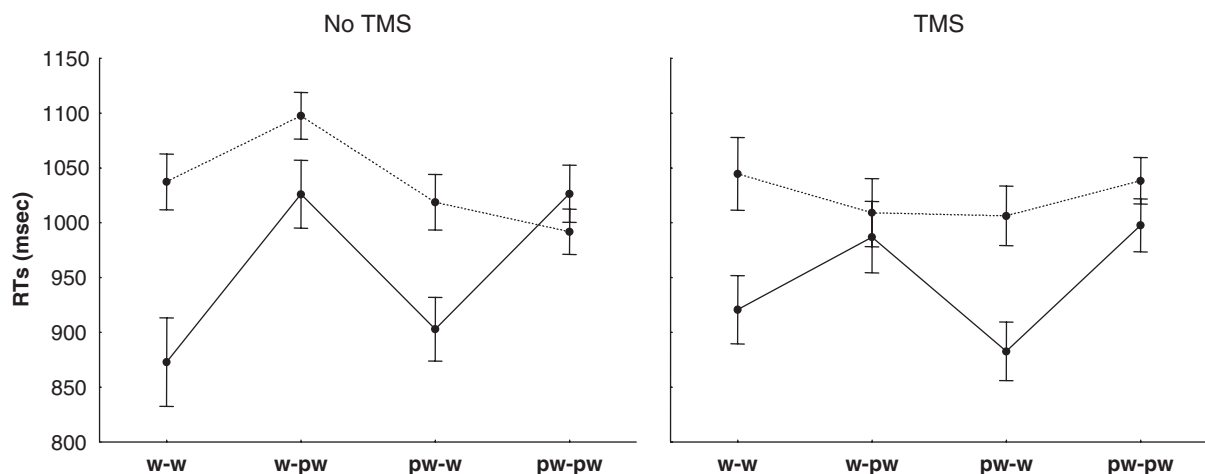


Fig. 5. Reaction times (RTs, msec \pm SEM) for the lexical decision during the phonological priming task with and without transcranial magnetic stimulation (TMS) between prime and target. Solid line: conditions in which prime and target share a rhyme. Dashed line: no rhyme. W-W, prime-word/target-word; W-PW, prime-word/target-pseudoword; PW-W, prime-pseudoword/target-word; PW-PW, prime-pseudoword/target-pseudoword.

phonological processing (at least in production) we decided to use a phonological paradigm in a new experiment: the “phonological priming” task. Phonological priming effect refers to the fact that a target word is recognized faster when it is preceded by a prime word, sharing with it the last syllable (rhyming effect, Emmorey, 1989). In a single pulse TMS experiment (see Fadiga et al., in press) we therefore stimulated participants’ inferior frontal cortex while they were performing a phonological priming task. Subjects were instructed to carefully listen to a sequence of acoustically presented pairs of verbal stimuli (dysyllabic “cvcv” or “cvccv” words and pseudowords) in which the final phonological overlap was present (rhyme prime) or, conversely, not present. The task of the subjects was to make a lexical decision on the second stimulus (target) by pressing with either the index or the middle finger one of two buttons whether the target was a word or a pseudoword. The pairs of verbal stimuli belonged to four categories, which differed for their lexical content in the prime and in the target (prime-word/target-word (W-W), prime-word/target-pseudoword (W-PW), prime-pseudoword/target-word (PW-W), prime-pseudoword/target-pseudoword (PW-PW)). Each category contained both rhyming and non-rhyming pairs. In some randomly selected trials, we

administered single pulse TMS in correspondence of left BA44 (Broca’s region, localized by using “Neurocompass,” a frameless stereotactic system built in our laboratory) during the interval (20 ms) between prime and target stimuli.

In trials without TMS, there were three main results (Fig. 5): (i) strong and statistically significant facilitation (phonological priming effect) when W-W, W-PW, PW-W pairs are presented; (ii) no phonological priming effect when the PW-PW pair is presented; (iii) faster responses when the target is a word rather than a pseudoword (both in W-W and PW-W).

An interesting finding emerges from the analysis of these results: The presence or absence of lexical content modulates the phonological priming effect. When neither the target nor the prime has access to the lexicon (PW-PW pair) the presence of the rhyme does not facilitate the recognition of the target. In other words, in order to have a phonological effect it is necessary to have access to the lexicon.

In trials with TMS delivery, only W-PW pairs were affected by brain stimulation, the W-PW pair behaving exactly as the PW-PW one. This finding suggests that the stimulation of the Broca’s region might have affected the lexical property of the prime (i.e., the meaningfulness of the stimulus). As

1 consequence, the impossibility to access the lexi- 1
 2 con determines the absence of the phonological 2
 3 effect. According to our interpretation, the TMS- 3
 4 related effect is absent in the W–W and PW–W 4
 5 pairs because of the presence of a meaningful (W) 5
 6 target. The finding that TMS administered on 6
 7 Broca’s region during phonological priming para- 7
 8 digm influences the rhyming effect only in the case 8
 9 of W–PW pairs poses a theoretical problem. In our 9
 10 previous TMS experiment on motor facilitation 10
 11 during speech listening (Fadiga et al., 2002) we 11
 12 have found cortical facilitation during listening of 12
 13 both words and pseudowords. This discrepancy 13
 14 suggests that a cortical area different from Broca’s 14
 15 one should be involved in such a “low level” mo- 15
 16 tor resonance. Its localization will be the argument 16
 17 of our future experimental work. 17

18 By summarizing the experimental evidence we 18
 19 presented here, we can claim that the activation of 19
 20 Broca’s region during speech processing, more 20
 21 than indicating a specific role of this area, may 21
 22 reflect its general involvement in meaningful action 22
 23 recognition. This possibility is based on the obser- 23
 24 vation that, in addition to speech-related activa- 24
 25 tion, this area is activated during observation of 25
 26 meaningful hand or mouth actions. Speech repre- 26
 27 sents a particular case of this general framework: 27
 28 among meaningful actions, phonoarticulatory ges- 28
 29 tures are meaningful actions conveying words. The 29
 30 consideration that Broca’s area is the human ho- 30
 31 molog of the monkey mirror neurons area opens 31
 32 the possibility that human language may have 32
 33 evolved from an ancient ability to recognize visu- 33
 34 ally or acoustically perceived actions performed 34
 35 by others (Rizzolatti and Arbib, 1998). 35

36 The motor representation of hand/mouth ac- 36
 37 tions present in Broca’s area, which derives from 37
 38 the execution/observation (hearing) matching sys- 38
 39 tem already present in monkeys, may have given to 39
 40 this area the capability to deal with verbal com- 40
 41 munication because of its twofold involvement 41
 42 with motor goals: during execution of own actions 42
 43 and during perception of others’ ones. Our hy- 43
 44 pothesis is that the original role played by this re- 44
 45 gion in generating/extracting action meanings 45
 46 might have been generalized during evolution giv- 46
 47 ing to this area the capability to deal with mean- 47
 48 ings (and rules) sharing with the motor system

1 similar hierarchical and sequential structures. Re- 1
 2 cent data from our laboratory on frontal aphasic 2
 3 patients are in line with this idea (see Fadiga et al., 3
 4 in press). 4

5 **A model of area F5 and of the mirror-neurons** 5 6 **system** 6

7 This section proposes a model of the mirror-neu- 7
 8 rons system, whose components are in general 8
 9 agreement with the functional properties of area 9
 10 F5 and with the knowledge on the connections 10
 11 that this area maintains with other cortical re- 11
 12 gions, which describes how the mirror-neurons 12
 13 system intervenes in action recognition (Metta et 13
 14 al., 2006). 14

15 It is known that F5 is part of a larger circuit 15
 16 comprising various areas in the parietal lobe (a 16
 17 large reciprocal connection with anterior intrapa- 17
 18 rietal area, AIP), indirectly from superior tempo- 18
 19 ral sulcus (STS), and other premotor and frontal 19
 20 areas. Moreover, it is strongly involved in the 20
 21 generation and control of action indirectly through 21
 22 primary motor cortex (F1), and directly by pro- 22
 23 jecting to motor and medullar interneurons in the 23
 24 spinal cord (see Luppino and Rizzolatti, 2000). 24

25 Our model of area F5 revolves around two con- 25
 26 cepts that are certainly related to the evolution and 26
 27 development of this unique area of the brain. 27
 28 Firstly, we posit that the mirror-neurons system 28
 29 did not appear brand new in the brain but likely 29
 30 evolved from a pre-existing structure devoted 30
 31 solely to the control of grasping action. The rea- 31
 32 sons for this claim are to be found in the large 32
 33 percentage of motor neurons in F5 (70%) com- 33
 34 pared to those that have also visual responses. 34
 35 Secondly, we attribute a fundamental role to ca- 35
 36 nonical neurons — and in general that of contex- 36
 37 tual information specifying the action goal — in 37
 38 the development of the mirror neurons. Since 38
 39 purely motor, canonical, and mirror neurons are 39
 40 found together in F5, it is very plausible that local 40
 41 connections determine at least in part the activa- 41
 42 tion of F5. 42

43 Our model follows a forward-inverse approach 43
 44 that has been also proposed in computational mo- 44
 45 tor control theory (Kawato et al., 1987; Wolpert 45
 46 47

and Miall, 1996) and for explanatory purpose it can be divided into two parts. The first part describes what happens in the actor's brain, the second what happens in the observer's brain when watching another acting individual. As we will see the same structures are used both when acting and when observing an action.

The agent's point of view

We shall consider first what happens from the actor's point of view (see Fig. 6). In her perspective,

decision to undertake a particular action is attained by the convergence in area F5 of many factors including the contextual- (by signals from parietal and frontal areas) and object-related information (canonical neurons). Object and context bias the activation of a specific motor plan, which specifies the goal of the motor system in motor terms and, we generally suppose, it includes temporal information. Our model hypothesize that action specification is initially "described" in frontal areas in some internal reference frame and then

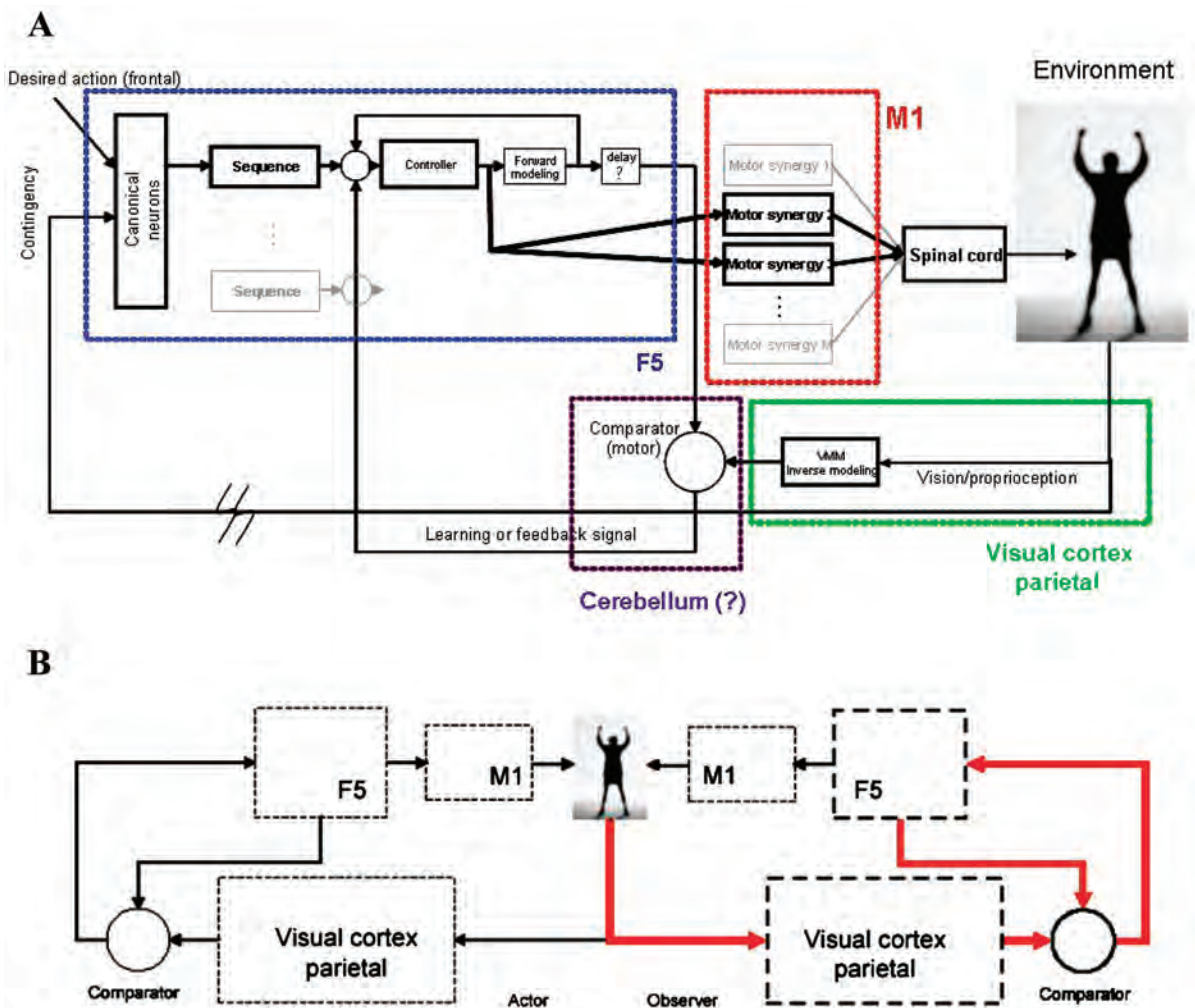


Fig. 6. Model schematics (see text for explanations). (A) Organization of the motor system during execution. (B) The same model working during action observation.

1 transformed into the motor plan by an appropriate
2 controller in F5.

3 The action plan unfolds mostly open loop (i.e.,
4 without employing feedback). A form of feedback
5 (closed loop) is required though to counteract dis-
6 turbances and to learn from mistakes. This is ob-
7 tained by relying on a forward or direct model that
8 predicts the outcome of the action as it unfolds in
9 real time. The output of the forward model can be
10 compared with the signals derived from sensory
11 feedback, and differences accounted for (the cere-
12 bellum is believed to have a role in this) (Miall et
13 al., 1993; Wolpert and Miall, 1996). A delay mod-
14 ule is included to take into account the different
15 propagation times of the neural pathways carrying
16 the predicted and actual outcome of the action.
17 Note that the forward model is relatively simple,
18 predicting only the motor output in advance: Since
19 motor commands are generated internally it is rel-
20 atively easy to imagine a predictor for this signals.

21 The inverse model (Visuo-Motor Map, VMM)
22 is much more complicated since it maps sensory
23 feedback (vision mainly) back into motor terms.
24 Visual feedback clearly includes both the hand-re-
25 lated information (STS) and the object informa-
26 tion (AIP, IT, and canonical neurons). Finally the
27 predicted and the sensory signals arising from ac-
28 tion execution are compared and the feedback er-
29 ror sent back to the controller. The mismatch
30 between the planned and actual action can either
31 be used to compensate on the fly by means of a
32 feedback controller, or to adjust over longer pe-
33 riods of time through learning (Kawato et al.,
34 1987).

35 The output of area F5, finally activates the mo-
36 tor neurons in the spinal cord (directly or indi-
37 rectly through motor synergies) to produce the
38 action. This is indicated by a connection to ap-
39 propriate muscular synergies representing the spi-
40 nal cord circuits.

41 Learning of the direct and inverse models can be
42 carried out during ontogenesis by a procedure of
43 self-observation and exploration of the state space
44 of the system: grossly speaking, simply by “de-
45 tecting” the sensorial consequences of motor com-
46 mands.

47 Learning of the affordances of objects (the ca-
48 nonical neurons response) with respect to grasping

1 can also be achieved autonomously by a trial and
2 error procedure, which explores the consequences
3 of trying many different actions of the agent’s
4 motor repertoire (different grasp types) to differ-
5 ent objects. This includes things such as discover-
6 ing that small objects are optimally grasped by a
7 pinch or precision grip, while big and heavy ob-
8 jects require a power grasp.

The observer’s point of view

9
10
11 In the observer situation motor and proprioceptive
12 information is not directly available. The only
13 readily available information is vision or sound.
14 The central assumption of our model is that the
15 structure of F5 could be co-opted in recognizing
16 the observed actions by transforming visual cues
17 into motor information as before. In practice the
18 inverse model is accessed by visual information,
19 since the observer is not acting herself, visual in-
20 formation directly reaches in parallel the sensori-
21 motor primitives in F5. Only some of them are
22 actually activated because of the “filtering” effect
23 of the canonical neurons and of other contextual
24 information (possibly at a higher level, knowledge
25 of the actor, plausibility of the hand posture, etc.).
26 This procedure could be used then to recognize the
27 action by measuring the most active motor prim-
28 itive. Thus, in our model, many factors, including
29 the affordances of the target object, determine the
30 recognition and interpretation of the observed ac-
31 tion.

Ontogenesis of mirror neurons

32
33
34
35
36
37 Our model gives us also the possibility to hypoth-
38 esize the ontogenesis of mirror neurons. First of
39 all, the inverse model, the VMM, can be learned
40 through a procedure of self-exploration. Motor
41 commands and correlated visual information are
42 readily available to the developing infant. It is easy
43 to imagine a procedure that learns the inverse
44 model on the basis of this information.

45
46
47 On the top of the VMM, it is plausible that the
48 canonical representation is acquired via the ma-
49 nipulation of a large set of different objects. F5
50 canonical neurons represent an association

1 between objects' physical properties and the actions they afford: e.g., a small object affords a
 3 precision grip, or a coffee mug affords being grasped by the handle. The understanding of object
 5 properties and the goal of actions is subsequently fundamental for disambiguating visual
 7 information. In fact, certain actions are more likely to be applied to a particular object, and
 9 certain objects are more likely to be used in certain actions. A link between action and effects can be
 11 traced backward on the basis of our experience: To obtain the effects we have to apply the same action
 13 that earlier led to those effects.

15 Bearing this in mind, when observing some other individual's actions; our understanding can be
 17 framed in the same terms: When I see someone grasping a mug full of coffee by the handle, I know
 19 that that precise affordance is the most suitable for drinking. If the same mug is empty and I see the
 21 agent grasping it by inserting the fingers into it, I can hypothesize that she is going to wash it. Consequently,
 23 I can recognize and also predict the outcome of the action on the basis of the link between the contextual
 25 information, the type of affordance, and the knowledge of object's properties. It is plausible that a mirror
 27 representation derives from the association between the visual information of others' actions and the action-
 29 effects link. To obtain this association, however, it is necessary that the observed consequences of an
 31 action are recognized as similar in the self or the other individual acting. Only if this happens, the
 33 association between the canonical response and the mirror one can then be made.

37 ***Role of motor information in the action recognition process***

39 The simplest way of confirming the hypothesis that motor representations are the basis of action
 41 recognition is to equip a computer with means of "acting" on objects, collect visual and motor data
 43 and build a recognition system that embeds some of the principles of operation that we identified in
 45 our model (see Fig. 6). In particular, the hypothesis we would like to test is whether the extra in-
 47 formation available during learning (e.g.,

1 kinesthetic and tactile) can improve and simplify the recognition of the same actions when they are
 3 just observed: i.e., when only visual information is available. Given the current limitations of robotic
 5 systems the simplest way to provide "motor awareness" to a machine is by recording grasping
 7 actions of human subjects from multiple sources of information including joint angles, spatial position
 9 of the hand/fingers, vision, and touch.

11 For this purpose we assembled a computerized system composed of a data glove (CyberGlove by
 13 Immersion), a pair of CCD cameras (Watek 202D), a magnetic tracker (Flock of bird, Ascension),
 15 and two touch sensors (FSR). Data was sampled at frame rate, synchronized, and stored to disk
 17 by a Pentium class PC. The cyber glove has 22 sensors and allows recording the kinematics of the
 19 hand at up to 112 Hz. The tracker was mounted on the wrist and provides the position and the orientation
 21 of the hand in space with respect to a base frame. The two touch sensors were mounted on the
 23 thumb and index finger to detect the moment of contact with the object. Cameras were mounted
 25 at appropriate distance with respect to their focal length to acquire the execution of the whole grasping
 27 action with maximum possible resolution.

29 The glove was lightweight and did not limit any way the movement of the arm and hand. Data
 31 recording was carried out with the subject sitting comfortably in front of a table and performing
 33 grasping actions naturally toward objects approximately at the center of the table. Data recording
 35 and storage was carried out through a custom-designed application; Matlab was employed for post-
 37 processing.

39 We collected a large data set and processing was then performed off-line. The selected grasping
 41 types were: power grasp-cylindrical, power grasp-spherical, and precision grasp. Since the goal was
 43 to investigate to what extent the system could learn invariances across different grasping types by
 45 employing motor information for classification, the experiment included gathering data from a
 47 multiplicity of viewpoints. The database contained objects, which afford several grasp types to assure
 that recognition cannot simply rely on exclusively extracting object features. Rather, according to
 our model, this is supposed to be a confluence of

1 object recognition (canonical neurons) with hand
visual analysis (STS).

3 A set of three objects was employed: a small
5 glass ball, a parallelepiped, and a large sphere.
7 Each grasping action was recorded from six differ-
9 ent subjects (right handed, age 23–29, male/female
11 equally distributed), and moving the cameras to 12
13 different locations around the subject including
two different elevations with respect to the table
top which amounts to 168 sequences per subject.
Each sequence contained images of the scene from
the two cameras synchronized with the cyber glove
and the magnetic tracker data.

15 The visual features were extracted from pre-
17 processed image data. The hand was segmented
19 from the images through a simple color segmen-
21 tation algorithm. The bounding box of the seg-
23 mented region was then used as a reference frame
25 to map the view of the hand to a standard size. The
orientation of the color blob in the image was also
used to rotate the hand to a standard orientation.
This data set was then filtered through Principal
Component Analysis (PCA) by maintaining only a
limited set of eigenvectors corresponding to the
first 2 to 15 largest eigenvalues.

27 One possibility to test the influence of motor
29 information in learning action recognition is to
31 contrast the situation where motor-kinesthetic in-
formation is available in addition to visual infor-
mation with the control situation where only
visual information is available.

33 In the “motor space” session we used the output
35 of the VMM (see the model schematics) and thus
37 employed motor features for classification. The
VMM was approximated from data by using a
simple feedforward neural network with sigmoidal
units trained with backpropagation. The input of
the VMM was the vector of the mapping of the
images onto the space spanned by the first N PCA
vectors; the output was the vector of joint angles
acquired from the data glove. In the “visual space”
session the classification was performed in visual
space directly.

45 Classification was always performed by training
a Bayesian classifier. In this formulation we iden-
47 tified the likelihood term with the activity of F5
motor neurons (probability of seeing certain fea-
tures given the performed action and target object)

1 and the priors with the canonical neurons (prob-
3 ability of using a certain action on a given object).
5 The classifier then applies a MAP criterion (max-
7 imum a posteriori) by computing the unnormal-
9 ized posterior probability and taking the
11 maximum over the possible actions.

13 The results of the experiment are reported in
15 Table 1.

17 Different sequences were used during the train-
19 ing and the testing phases. During the training
21 phase, 24 sequences from only one point of view
23 were used in the motor space session, while 64 se-
25 quences from all the four different points of view
27 were used in the visual space session. Thus, the
classifier was trained with the maximum available
data only in the latter session. During the testing
phase, 96 sequences from four points of view were
used in the motor space session, and 32 sequences
from four points of view in the visual space one.

29 The clearest result of this experiment is that the
31 classification in motor space is easier and thus the
33 classifier performs better on the test set. Moreover,
35 the distribution of the data is more “regular” (the
37 likelihood term is simpler) in motor space than in
visual space. This is to be expected since the vari-
ation of the visual appearance of the hand is
larger and depends strongly on the point of view,
while the sequence of joint angles tends to be the
same across repetitions of the same action. It is
also clear that in the experiment the classifier is
much less concerned with the variation of the data

39 Table 1. Summary of the results of the experiment testing the
41 model

	Motor space session	Visual space session
Training		
No. of sequences	24 (+ VMM)	64
No. of points of view	1	4
Classification rate (on the training set) (%)	98	97
Test		
No. of sequences	96	32
No. of points of view	4	4
Classification rate (%)	97	80

1 since this variation has been taken out by the
2 VMM.

3 Overall, our interpretation of these results is
4 that by mapping in motor space first we are al-
5 lowing the classifier to choose features that are
6 much better suited for performing optimally,
7 which in turn facilitates generalization. The same
8 is not true in visual space.

11 *The interaction with the environment and the 12 development of mirror-like representation*

13 In order to show that, according to our model, a
14 mirror-neuron-like representation could be ac-
15 quired by simply relying on the information ex-
16 changed during the interaction with the
17 environment, we set forth to the implementation
18 of a complete experiment on a humanoid robot
19 called Cog (Brooks et al., 1999). This was an up-
20 per-torso human shaped robot with 22 degrees of
21 freedom distributed along the head, arms, and
22 torso. It lacked hands, it had instead simple flip-
23 pers that could use to push and prod objects. It
24 could not move from its stand so that the objects it
25 interacted with had to be presented to the robot by
26 a human experimenter. The robot was controlled
27 by a distributed parallel control system based on a
28 real-time operating system and running on a set of
29 Pentium based computers. The robot was
30 equipped with cameras (for vision), gyroscopes
31 simulating the human vestibular system, and joint
32 sensors providing information about the position
33 and torque exerted at each joint.

34 Since the robot did not have hands, it could not
35 really grasp objects from the table. Nonetheless
36 there are other actions that can be employed in
37 exploring the physical properties of objects, such
38 as touching, poking, prodding, and sweeping.
39 Moreover, since the interaction of the robot's flip-
40 per with objects was limited, we employed rolling
41 objects that show a characteristic behavior de-
42 pending on how they are approached: a toy car, an
43 orange juice bottle, a ball, and a colored toy cube.
44 The robot's motor repertoire besides reaching
45 consisted of four different stereotyped approach
46 movements covering a range of directions of about
47 180° around the object. The sequence of images

1 acquired during reaching for the object, the mo-
2 ment of impact, and the effects of the action were
3 measured following the approach in Fitzpatrick
4 (2003) and Metta and Fitzpatrick (2003).

5 The experiment consisted in presenting repeti-
6 tively each of the four objects mentioned above to
7 the robot. During this stage also other objects were
8 presented at random; the experiment ran for sev-
9 eral days and sometimes people walked by the ro-
10 bot and managed to make it poke the most
11 disparate objects. For each successful trial, the ro-
12 bot "stored" the result of the segmentation of the
13 object from the background, the object's principal
14 axis which was selected as representative shape
15 parameter, the action — initially selected ran-
16 domly from the set of four approach directions —
17 and the movement of the center of mass of the
18 object for some hundreds milliseconds after the
19 impact was detected. We grouped data belonging
20 to the same object by employing a color-based
21 clustering technique. In fact in our experiments the
22 toy car was mostly yellow in color, the ball violet,
23 the bottle orange, etc.

24 It is possible to describe object behavior in vis-
25 ual terms by estimating the probability of observ-
26 ing object motion relative to the object's own
27 principal axis. Intuitively, this gives information
28 about the rolling properties of the different ob-
29 jects: e.g., the car tends to roll along its principal
30 axis, the bottle at right angle with respect to the
31 axis. For the purpose of generating actions a de-
32 scription of the geometry of poking is required and
33 has to go with the description of the object rolling
34 behavior. This can be easily obtained by collecting
35 many samples of generic poking actions and esti-
36 mating the average direction of displacement of
37 the object.

38 Having a visual and a "pragmatic" description
39 of objects, it is now possible to test whether this
40 information can be re-used to make the robot
41 "optimally" poke (i.e., selecting an action that
42 causes maximum displacement) a known object. In
43 practice the same color clustering procedure is
44 used for localizing and recognizing the object, to
45 determine its orientation on the table, its affor-
46 dance, and finally to select the action that it is most
47 likely to elicit the principal affordance (roll).

1 A simple qualitative test of the performance determined that out of 100 trials the robot made 15
3 mistakes. Further analysis showed that 12 of the 15 mistakes were due to poor control of reaching
5 (e.g., the flipper touched the object too early bringing it outside the field of view), and only three
7 to a wrong estimate of the orientation.

9 Although crude, this implementation shows that with little pre-existing structure the robot could
11 acquire the crucial elements for building knowledge of objects in terms of their affordances. Given
13 a sufficient level of abstraction, our implementation is close to the response of canonical neurons
15 in F5 and their interaction with neurons observed in AIP that respond to object orientation (Sakata
17 et al., 1997).

19 At this point, we can test whether knowledge about object-directed actions can be reused in interpreting
21 observed actions performed perhaps by a human experimenter. According to our model, whereas the robot
23 identified the motion of the object because of a certain action applied to it, during action observation
25 it could backtrack and derive the type of action from the observed motion of the object. In fact, the
27 same segmentation procedure could visually interpret poking actions generated by a human as well as
29 those generated by the robot.

31 Thus, observations can be converted into interpreted actions. The action whose effects are closest
33 to the observed consequences on the object (which we might translate into the goal of the action) is
35 selected as the most plausible interpretation given the observation. Most importantly, the interpretation
37 reduces to the interpretation of the “simple” kinematics of the goal and consequences of the action
39 rather than to understanding the “complex” kinematics of the human manipulator. The robot
41 understands only to the extent it has learned to act.

43 In order to test this possibility we verified whether the robot could imitate the “goal” of a
45 poking action. The step is indeed small since most of the work is actually in interpreting observations.
47 Imitation was generated in the following by replicating the latest observed human movement with
respect to the object and irrespective of its orientation. For example, in case the experimenter

1 poked the toy car sideways, the robot imitated him/her by pushing the car sideways (for further
3 details, see Metta and Fitzpatrick, 2003).

5 In summary, the results from our experiments seem to confirm two facts of the proposed model:
7 first, that motor information plays a role in the recognition process — as would be following the
9 hypothesis of the implication of feedback signals into recognition — and, second, that a mirror-like
11 representation can be developed autonomously on the basis of the interaction between an individual
13 and the environment.

17 Conclusions

19 In this paper, starting from known experiments in the monkey, we reviewed the evidence for the
21 existence of a mirror-neurons system in humans. We highlighted the fact that the mirror system is not a
23 passive observer that only “resonates” with the incoming sensory stimulation but rather it works
25 in predicting the future course of action, in filling gaps, and in merging the available evidence for the
27 plausibility of the ongoing observed action. This last aspect includes contextual information which
29 in turn represents the goal of the action and eventually its meaning. We also reviewed the link between
31 the mirror system and speech drawing a parallel between vision and sound but ultimately showing that
33 both impinge on the motor system. Finally, we covered, although briefly, some computation modeling
35 of the mirror system which can be used to clarify certain aspects of the functioning of the biological
37 counterpart. Although still partial, this implementation shows that, in principle, the acquisition of the
39 mirror neurons structure is the almost natural outcome of the development of a control system for
41 grasping. Also, we have put forward a plausible sequence of learning phases involving the interaction
43 between canonical and mirror neurons. This, we believe, is well in accordance with the evidence
45 gathered by neurophysiology. In conclusion, we have embarked in an investigation that is somewhat
47 similar to Liberman’s artificial speech recognition attempts. Perhaps, also this time, the mutual rapprochement of

neural and engineering sciences might lead to a better understanding of brain functions.

Acknowledgments

This work has been supported by European Commission grants ROBOT-CUB, NEUROBOTICS and CONTACT, by Italian Ministry of Education grants and by Fondazione Cassa di Risparmio di Ferrara.

References

- Arbib, M.A. (1997) From visual affordances in monkey parietal cortex to hippocampo-parietal interactions underlying rat navigation. *Philos. Trans. R. Soc. Lond. B Biol. Sci.*, 352: 1429–1436.
- Barbas, H. and Pandya, D.N. (1987) Architecture and frontal cortical connections of the premotor cortex (area 6) in the rhesus monkey. *J. Comp. Neurol.*, 256: 211–228.
- Binkofski, F., Buccino, G., Posse, S., Seitz, R.J., Rizzolatti, G. and Freund, H. (1999) A fronto-parietal circuit for object manipulation in man: evidence from an fMRI-study. *Eur. J. Neurosci.*, 11: 3276–3286.
- Borroni, P., Montagna, M., Cerri, G. and Baldissera, F. (2005) Cyclic time course of motor excitability modulation during the observation of a cyclic hand movement. *Brain Res.*, 1065: 115–124.
- Broca, P. (1861) Remarques sur le Siège de la Faculté du Langage Articulé, Suivies d'une Observation d'aphemie (Perte de la Parole). *Bulletin de la Société Anatomique de Paris*, 6: 330–357.
- Brooks, R.A., Breazeal, C., Marjanovi, M., Scassellati, B. and Williamson, M.M. (1999) The Cog project: Building a humanoid robot. In: Nehaniv C.L. (Ed.), *Computation for Metaphors, Analogy and Agents*. Springer-Verlag, pp. 52–87.
- Buccino, G., Binkofski, F., Fink, G.R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R.J., Zilles, K., Rizzolatti, G. and Freund, H.J. (2001) Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur. J. Neurosci.*, 13: 400–404.
- Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., Porro, C.A. and Rizzolatti, G. (2004) Neural circuits involved in the recognition of actions performed by nonconpecifics: an FMRI study. *J. Cogn. Neurosci.*, 16: 114–126.
- Campbell, R., MacSweeney, M., Surguladze, S., Calvert, G., McGuire, P., Suckling, J., Brammer, M.J. and David, A.S. (2001) Cortical substrates for the perception of face actions: an fMRI study of the specificity of activation for seen speech and for meaningless lower-face acts (gurning). *Brain Res. Cogn. Brain Res.*, 12: 233–243.
- Cochin, S., Barthelemy, C., Lejeune, B., Roux, S. and Martin-eau, J. (1998) Perception of motion and qEEG activity in human adults. *Electroencephalogr. Clin. Neurophysiol.*, 107: 287–295.
- Craighero, L., Bonetti, F., Massarenti, L., Canto, R., Fabbri Destro M. and Fadiga L. (in press) Temporal prediction of touch instant during observation of human and robot grasping. *Brain Res. Bull.*
- Decety, J., Grezes, J., Costes, N., Perani, D., Procyk, E., Grassi, F., Jeannerod, M. and Fazio, F. (1997) Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain*, 120: 1763–1777.
- Emmorey, K.D. (1989) Auditory morphological priming in the lexicon. *Lang. Cognitive Proc.*, 4: 73–92.
- Fadiga, L., Craighero, L., Buccino, G. and Rizzolatti, G. (2002) Speech listening specifically modulates the excitability of tongue muscles: a TMS study. *Eur. J. Neurosci.*, 15: 399–402.
- Fadiga, L., Craighero, L., Fabbri Destro, M., Finos, L., Cottillon-Williams, N., Smith, A.T. and Castiello, U. (2006) Language in shadow. *Soc. Neurosci.*, 1: 77–89.
- Fadiga, L., Fogassi, L., Pavesi, G. and Rizzolatti, G. (1995) Motor facilitation during action observation: a magnetic stimulation study. *J. Neurophysiol.*, 73: 2608–2611.
- Fadiga, L., Roy, A.C., Fazio, P. and Craighero, L. (in press) From hand actions to speech: evidence and speculations. In: Haggard P., Rossetti Y. and Kawato M. (Eds.), *Sensorimotor Foundations of Higher Cognition. Attention and Performance*. Oxford University Press, Oxford.
- Fitzpatrick, P. (2003) From First Contact to Close Encounters: A developmentally deep perceptual system for a humanoid robot. Unpublished PhD thesis, MIT, Cambridge, MA.
- Gallese, V., Fadiga, L., Fogassi, L. and Rizzolatti, G. (1996) Action recognition in the premotor cortex. *Brain*, 119: 593–609.
- Gangitano, M., Mottaghy, F.M. and Pascual-Leone, A. (2001) Phase-specific modulation of cortical motor output during movement observation. *Neuroreport*, 12: 1489–1492.
- Gangitano, M., Mottaghy, F.M. and Pascual-Leone, A. (2004) Modulation of premotor mirror neuron activity during observation of unpredictable grasping movements. *Eur. J. Neurosci.*, 20: 2193–2202.
- Grafton, S.T., Arbib, M.A., Fadiga, L. and Rizzolatti, G. (1996) Localization of grasp representations in humans by positron emission tomography. 2. Observation compared with imagination. *Exp. Brain Res.*, 112: 103–111.
- Grezes, J., Armony, J.L., Rowe, J. and Passingham, R.E. (2003) Activations related to “mirror” and “canonical” neurons in the human brain: an fMRI study. *Neuroimage*, 18: 928–937.
- Grezes, J., Costes, N. and Decety, J. (1998) Top down effect of the strategy on the perception of human biological motion: a PET investigation. *Cognitive Neuropsychol.*, 15: 553–582.
- Hamzei, F., Rijntjes, M., Dettmers, C., Glauche, V., Weiller, C. and Buchel, C. (2003) The human action recognition system and its relationship to Broca's area: an fMRI study. *Neuroimage*, 19: 637–644.

- 1 Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S.
and Rizzolatti, G. (1998) Activation of human primary mo-
3 tor cortex during action observation: a neuromagnetic study.
Proc. Natl. Acad. Sci. U.S.A., 95: 15061–15065.
- 5 Johnson-Frey, S.H., Maloof, F.R., Newman-Norlund, R., Far-
7 rer, C., Inati, S. and Grafton, S.T. (2003) Actions or hand-
object interactions? Human inferior frontal cortex and action
9 observation. *Neuron*, 39: 1053–1058.
- 11 Kawato, M., Furukawa, K. and Suzuki, R. (1987) A hierar-
chical neural-network model for control and learning of vol-
13 untary movement. *Biol. Cybern.*, 57: 169–185.
- 15 Kilner, J.M., Vargas, C., Duval, S., Blakemore, S.J. and Sirigu,
A. (2004) Motor activation prior to observation of a pre-
17 dicted movement. *Nat. Neurosci.*, 7: 1299–1301.
- 19 Kohler, E., Keysers, C., Umiltà, M.A., Fogassi, L., Gallese, V.
and Rizzolatti, G. (2002) Hearing sounds, understanding ac-
21 tions: action representation in mirror neurons. *Science*, 297:
846–848.
- 23 Liberman, A.M., Cooper, F.S., Shankweiler, D.P. and Stud-
dert-Kennedy, M. (1967) Perception of the speech code. *Psy-
25 chol. Rev.*, 74: 431–461.
- 27 Liberman, A.M. and Mattingly, I.G. (1985) The motor theory
of speech perception revised. *Cognition*, 21: 1–36.
- 29 Liberman, A.M. and Whalen, D.H. (2000) On the relation of
speech to language. *Trends Cogn. Sci.*, 4: 187–196.
- 31 Luppino, G. and Rizzolatti, G. (2000) The organization of the
frontal motor cortex. *News Physiol. Sci.*, 15: 219–224.
- 33 Matelli, M., Luppino, G. and Rizzolatti, G. (1985) Patterns of
cytochrome oxidase activity in the frontal agranular cortex of
35 the macaque monkey. *Behav. Brain Res.*, 18: 125–136.
- 37 Metta, G. and Fitzpatrick, P. (2003) Early integration of vision
and manipulation. *Adapt. Behav.*, 11: 109–128.
- 39 Metta, G., Sandini, G., Natale, L., Craighero, L. and Fadiga,
L. (2006) Understanding mirror neurons: A bio-robotic ap-
41 proach. *Interact. Stud.*, 7: 197–232.
- 43 Miall, R.C., Weir, D.J., Wolpert, D.M. and Stein, J.F. (1993) Is
the cerebellum a Smith predictor? *J. Motor Behav.*, 25:
45 203–216.
- 47 Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V. and
Rizzolatti, G. (1997) Object representation in the ventral
premotor cortex (area F5) of the monkey. *J. Neurophysiol.*,
78: 2226–2230.
- Nelissen, K., Luppino, G., Vanduffel, W., Rizzolatti, G. and
Orban, G.A. (2005) Observing others: multiple action repre-
sentation in the frontal lobe. *Science*, 310: 332–336.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V. and Ri-
zzolatti, G. (1992) Understanding motor events: a neuro-
physiological study. *Exp. Brain Res.*, 91: 176–180.
- Petrides, M. (2006) Broca's area in the human and the nonhu-
man primate brain. In: Grodzinsky Y. and Amunts K. (Eds.),
Broca's Region. Oxford University Press, New York, pp.
31–46.
- Petrides, M. and Pandya, D.N. (1994) Comparative architec-
tonic analysis of the human and the macaque frontal cortex.
In: Boller F., Spinnler H. and Hender J.A. (Eds.), *Handbook
of Neuropsychology*. Elsevier, Amsterdam.
- Rizzolatti, G. and Arbib, M.A. (1998) Language within our
grasp. *Trends Neurosci.*, 21: 188–194.
- Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Lup-
pino, G. and Matelli, M. (1988) Functional organization of
inferior area 6 in the macaque monkey. II. Area F5 and the
control of distal movements. *Exp. Brain Res.*, 71: 491–507.
- Rizzolatti, G. and Craighero, L. (2004) The mirror-neuron sys-
tem. *Annu. Rev. Neurosci.*, 27: 169–192.
- Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu,
E., Perani, D. and Fazio, F. (1996) Localization of grasp
representations in humans by PET: 1. Observation versus
execution. *Exp. Brain Res.*, 111: 246–252.
- Rizzolatti, G., Fogassi, L. and Gallese, V. (2001) Neurophys-
iological mechanisms underlying the understanding and im-
itation of action. *Nat. Rev. Neurosci.*, 2: 661–670.
- Rizzolatti, G. and Gentilucci, M. (1988) Motor and visual-mo-
tor functions of the premotor cortex. In: Rakic P. and Singer
W. (Eds.), *Neurobiology of Neocortex*. Wiley, Chichester,
pp. 269–284.
- Sakata, H., Taira, M., Kusunoki, M., Murata, A. and Tanaka,
Y. (1997) The TINS Lecture. The parietal association cortex
in depth perception and visual control of hand action. *Trends
Neurosci.*, 20: 350–357.
- Salmelin, R. and Hari, R. (1994) Spatiotemporal characteristics
of sensorimotor neuromagnetic rhythms related to thumb
movement. *Neuroscience*, 60: 537–550.
- Strafella, A.P. and Paus, T. (2000) Modulation of cortical ex-
citability during action observation: a transcranial magnetic
stimulation study. *Neuroreport*, 11: 2289–2292.
- Umiltà, M.A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L.,
Keysers, C. and Rizzolatti, G. (2001) I know what you are
doing: a neurophysiological study. *Neuron*, 31: 155–165.
- Watkins, K.E., Strafella, A.P. and Paus, T. (2003) Seeing and
hearing speech excites the motor system involved in speech
production. *Neuropsychologia*, 41: 989–994.
- Wolpert, D.M. and Miall, R.C. (1996) Forward models for
physiological motor control. *Neural Netw.*, 9: 1265–1279.