

Perception in action

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Abstract. For long time perception and action have been considered as separated and peripheral processes, devoid of any intrinsic cognitive value. Over the last years, however, this view has been challenged by several neurophysiological data. The aim of this paper is to provide an overview of some recent studies on the cortical visual and motor systems. In particular, we'll focus on the discovery (in the inferior parietal lobe and in the premotor cortex) of two different kinds of sensorimotor neurons that not only are involved in the motor control of actions, but also play an essential role in object categorizing and in action understanding. We'll argue that the functional properties of these kinds of neurons show the limits and abstractness of any strict dichotomy between perception and action, and pave the way to a requalification of some relevant philosophical perspectives on these issues. (www.actabiomedica.it)

Key words: Action, perception, cortical visual system, cortical motor system, mirror neurons

The action field of the physiology is not the abstract thought about nature. The physiology makes experience of nature in order to think it.

Johannes Müller

Introduction

For decades cognitive scientists and philosophers of mind have strictly separated perception and action, reducing them to marginal processes of a “disembodied” brain without biological roots. They thought that the main brain function was to compute mental representations and to execute cognitive tasks.

Susan Hurley (1, 2), almost mockingly, compared this view to a sandwich: perception and action would be the two slices of bread, separated one from the other and dependent, for their taste, on the rich filling, i.e. the high cognitive functions (intentions, desires, beliefs, etc.). According to Hurley's metaphor, such a view implies a rigid distinction of levels which would be involved in the processing of sensorial information in a linear and unidirectional way: i.e. perception → cognition → action.

In the following paragraphs we are going to show how over the last years several neurophysiological studies have offered us a very different description of brain architecture and functions. We are referring to the researches concerning cortical mechanisms underlying visual perception and sensorimotor transformations necessary for acting. These researches changed the standard view of the sensorial systems (visual *in primis*) and of the motor system as well, shading light on the mutual relationship between action and perception. Instead of tasteless “slices” of bread, action and perception became the basis of a new conception of the cognitive processes – no more abstractly considered from a computational point of view, but interpreted in terms of their embodied ties to acting and perceiving subjects.

Vision for action

The idea that the cortical visual system is far more complex than previously hypothesized, underlies some of the most debated models of the neural mechanisms of visual cognition.

By examining the selective effects of lesions in the brains of macaque monkeys, Leslie Ungerleider and Mortimer Mishkin (3) found that a damage in the inferotemporal lobe impaired the animals to discriminate objects of different colours, shapes, and textures, but not to perceive spatial relations, whereas a damage in the posterior parietal lobe impaired the animals to perform spatial tasks, but it left intact their ability in object discrimination. On the basis of this double dissociation and the reconsideration of previous anatomical data, Ungerleider and Mishkin concluded that the visual cortical areas are organized in two segregated and differentiated pathways: one (*ventral pathway*) connecting the primary visual cortex to the inferotemporal lobe and processing the information on visual object properties, the other (*dorsal pathway*) connecting the primary visual cortex to the posterior parietal lobe and processing the information on spatial relations among objects (Figure 1).

The Ungerleider and Mishkin's model, however, has been revised by David Milner and Melvyn Goodale (4). Through several experiments on a patient (D.F.) with extended lesions in the occipitotemporal areas, they showed that D.F. was deeply impaired in the visual recognition of the shape of presented objects, but she retained the ability to act on them. D.F. was able to grasp objects such as a ball or a stick whose shapes, sizes, and orientations she couldn't visually recognize. Milner and Goodale compared then the visual impairments of D.F. (known as visual form agnosia) with the visual deficits typical of optic ataxic

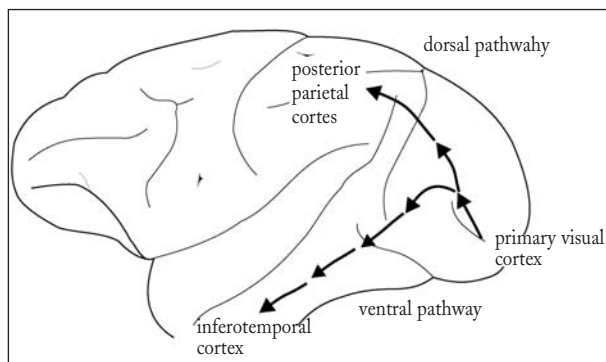


Figure 1. Lateral view of the macaque monkey brain showing the two visual pathways according to Ungerleider and Mishkin's (3) and Milner and Goodale's (4) models

patients. Optic ataxia is a disorder of visually guided arm movements toward a target produced from damages in the posterior parietal cortex. Unlike the visual form agnostic patients, the optic ataxic patients are deeply impaired to grasp objects whose shapes, sizes, and orientations they can visually recognize.

According to Milner and Goodale, such clinical data indicate that the fundamental functional difference between the ventral and dorsal pathways is not in the percept (object vs. space) resulting from the processing of visual information, as maintained Ungerleider and Mishkin, but in the use that the higher cortical areas made of the visual information encoded by the two pathways. The ventral pathway provides the visual information required for the object recognition: its function is what Milner and Goodale call "vision-for-perception". Conversely, the dorsal pathway processes the visual information necessary for the control of movements: its function is what they call "vision-for-action".

The main divergence between the Ungerleider and Mishkin's and the Milner and Goodale's models concerns the functional significance of the dorsal pathway. Ungerleider and Mishkin assume that visual perception is the exclusive function of the cortical visual system: even though in different ways, both the ventral pathway and the dorsal pathway code the visual information in merely perceptive terms. By contrast, in Milner and Goodale's view, the cortical visual system is not limited to perception, but it contributes also to the control of visually guided actions. The dorsal pathway converts automatically visual inputs into motor commands, enabling the visuomotor transformations requested for reaching and grasping objects.

No doubt, the Milner and Goodale's model provides insights into the functional architecture of the cortical visual system: it emphasizes the visuomotor properties of the posterior parietal lobe which had been studied by Vernon Mountcastle and co-workers in the mid-1970s (see, for example, 5); and on the other hand, it breaks definitively off with a consolidated tradition which for a long time had reduced the processing of visual information to perception.

More recent researches, however, have shown that the Milner and Goodale's model doesn't allow us

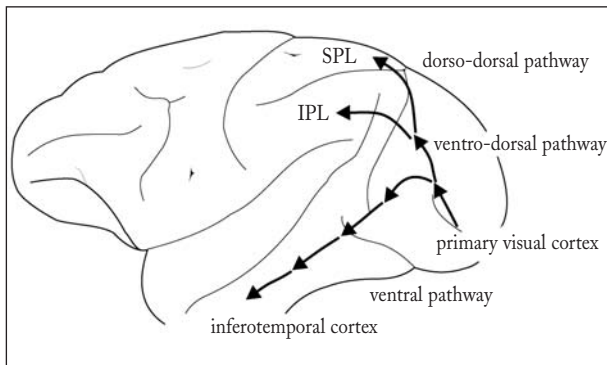


Figure 2. Lateral view of the macaque monkey brain showing the three visual pathways according to Rizzolatti and Matelli's (6) model. IPL: inferior parietal lobe; SPL: superior parietal lobe

to fully understand the functional range of the posterior parietal cortex yet. The latest studies of the anatomical connections and functional properties of the cortical areas forming the dorsal pathway suggest that it is actually composed by two distinct systems: a dorso-dorsal pathway, connecting the visual cortex to the superior parietal lobe, and a ventro-dorsal pathway, centred on some regions of the inferior parietal lobe and connecting the visual cortex to the ventral premotor cortex (6; figure 2). The dorso-dorsal pathway is quite exclusively involved in the organization of the motor activities, as claimed by Milner and Goodale for their dorsal pathway. On the contrary, the ventro-dorsal pathway is characterized by a complex of parieto-frontal circuits, whose sensorial and motor functions are hard to attribute only to the control of actions on line. As we shall see in the following pages, the analysis of such circuits not only sheds new light on the cortical mechanisms underlying the sensorimotor processes, but also reveals the limits and abstractness of any strict dichotomy between perception and action.

Grasping an espresso cup

Let's dwell on the parieto-frontal circuit involved in visuomotor transformations for hand movements executed under visual guidance such as grasping.

In a series of experiments with monkeys, Hideo Sakata and collaborators (7) showed that the anterior

intraparietal area (AIP) plays a crucial role in this respect. By using an experimental paradigm with three different tasks (grasping an object in the light, grasping an object in the dark, and object fixation without grasping it), they found that AIP neurons could be subdivided into three main classes: motor dominant neurons, visual and motor neurons, and visual dominant neurons. Motor dominant neurons fired during grasping both in the light and in the dark, but not during the mere object fixation. Visual and motor neurons fired during grasping both in the light and in the dark, and also during the mere object fixation. Visual dominant neurons fired during grasping in the light and object fixation, but not during grasping in the dark. In addition, many of AIP neurons were selective for object shapes and sizes: in particular, many of the AIP visual and motor neurons showed a significant congruency between the selectivity exhibited during objects grasping and the selectivity exhibited during the mere fixation of the same objects.

From the anatomical point of view, AIP is strongly reciprocally connected with an area, F5, localized in the rostral region of the ventral premotor cortex (8, 9). Some years ago, Giacomo Rizzolatti and his collaborators discovered that many of F5 neurons code a specific goal-directed action such as grasping, manipulating, holding, etc., rather than the single movements forming it (10, 11). Thus, for example, F5 neurons discharging during fingers and hand movement performed to grasp an object do not respond to similar movements made with other purposes (e.g. scraping). Furthermore, several F5 neurons fire during motor acts that share the same goal (e.g. grasping) but are performed with different effectors (the right hand, the left hand, or the mouth). Many F5 neurons are more specific and code also a particular kind of grip (e.g. precision grip, finger prehension, or whole hand prehension).

By assuming as classification criteria the effective motor acts, Rizzolatti and collaborators subdivided F5 neurons into main classes such as "grasping-with-the-hand-and-the-mouth neurons", "grasping-with-the-hand neurons", "holding neurons", "tearing neurons", etc. They proposed also to conceive F5 as a "vocabulary" of motor acts, whose "words" are represented by a given population of neurons: some "words" indicate

the general goal of an action (grasping, holding, tearing); others indicate the way to perform an action, specifying the effectors or the type of grip to be used. The functional meaning of such a motor vocabulary is almost twofold: first, by reducing the information about action to few elements (e.g. goal, effectors, type of grip), it simplifies the combined selection of movements and the control of their execution; second, it facilitates the link between a sensorial stimulus (e.g. an object, with a given shape and size) and the motor act better matching it.

Most interestingly, many F5 neurons not only discharge during purposeful hand/mouth movements, but also respond to visual stimuli. By using a paradigm similar to that used for AIP neurons, Murata and collaborators showed that a high percentage of the F5 neurons activated selectively in response to visual presentation of three-dimensional objects (12). For instance, they found neurons that strongly discharged during observation and grasping of a ring, but whose responses to other objects (e.g. plate, cone, cube, sphere) are modest or absent, and vice-versa. Like the AIP visual motor neurons, a considerable percentage of tested F5 neurons fired also during the mere object fixation, when it wasn't required to grasp it, and showed a strict congruency between their motor and visual responses. Neurons that discharged during a precision grip responded also to the simple observation of a small object, but didn't fire for a large one; on the contrary, neurons that discharged during a whole hand grip, responded also to the simple observation of a large object, but didn't fire for a small one.

The characteristics of AIP and F5 neurons suggest that these areas form a circuit crucially involved in transforming visual information into hand action such as grasping. As the pioneering studies by Marc Jeannerod (13, 14) have shown, grasping is characterised by two different phases: an initial phase, that involves a progressive opening and shaping of fingers according to the object intrinsic features (shape, size), and a final phase, characterized by a bending and closure of fingers until they match object. Not all visual information are relevant to hand preshaping. The selection of the type of grip depends on the shape and size of the parts of the object that allow us to grasp it with a hand (see also 15).

Let's take, for example, an espresso cup: during the initial opening phase, the fingers have to be tuned to the shape and size of its handle, its body or its upper border. Visual inputs concerning the handle, body, or upper border, therefore, have to be extracted from the global visual information on the cup. But that is not enough. To have an appropriate hand configuration, the visual inputs concerning the handle, body, or upper border have also to be coded in terms of the types of grip they allow.

Given the properties of AIP and F5 neurons, it is quite likely that the AIP neurons break down the visual information on the object (e.g. espresso cup) and select its portions (handle, body, or upper border) relevant to grasping. So parcelled, the information is sent to the F5 neurons, suggesting various grasping opportunities. Choosing one of them depends also on the inputs that F5 receives from the prefrontal lobe. These inputs concern purposes of grasping, motivations, etc. When you would like to drink some coffee, your hand usually takes the handle of the espresso cup with a precision grip. But when you simply want to move the espresso cup, you can take it with many other kinds of grip. Finally, in order to happen, the grasping possibility selected by F5 neurons has to be sent to primary motor cortex and subcortical centres, providing the necessary information for the execution and control of action (for more details see also 16, 17).

Back to the “bottom”

So far so good. The AIP-F5 circuit allows us to elucidate the cortical mechanism of visuomotor transformations connected to motor execution of visual guided hand actions such as grasping. But, as we pointed out before, many AIP and F5 neurons respond also to the mere observation of an object, even in absence of any explicit motor behaviour directed at it. How could we interpret such visual responses? How could we explain that the same neurons discharge as *motor* neurons in some conditions and as *visual* neurons in others?

According to Giacomo Rizzolatti and Vittorio Gallese, these motor and visual responses have the same functional meaning. In their words: “This com-

mon meaning is the representation of an action, or to use an old term, the ‘idea’ of an action. This idea, which indicates very precisely how to interact with an object, is evoked either endogenously [...] or exogenously when the monkey observes an object. In the latter case, if other contingencies are present, the idea of action becomes that action, otherwise it remains a pure potentiality” (18; see also 19).

The functions of AIP-F5 circuit, therefore, can’t be reduced to mere action control. The specificity of the visual responses of AIP and F5 neurons and their high congruency with the motor responses of the same neurons suggest that this circuit plays an essential role not only for action execution, but also for object perception. Whatever the observation of an object is followed by a motor act directed to it, AIP and F5 neurons code the visual properties concerning its shape and size in terms of the “ideas of action”, i.e. action potentialities, that they offer. The fact that the sight of an object determines the discharge of the same motor neurons that respond when the observer performs a given action on it (e.g. grasping) shows how in the cortical motor system perceiving and acting are strictly matched. Observing an object allows the observer to perceive directly the potential actions offered by the object itself. Object’s intrinsic properties such as its shape and size are not reducible to their visual configuration. Rather, as already suggested by James Gibson (20), they represent a rich and complex set of possible interactions that the perceived object *afford* the subject who perceives it. Both visual *affordances* and related potential actions are constitutive parts of the perception of an object, and contribute to determine its meaning.

Let’s go back to the espresso cup: the visual inputs on its handle, body, or upper border are coded by AIP neurons and then transformed into potential hand configurations by F5 neurons, even when the agent hasn’t any intention to grasp the cup. This means that the agent perceives the cup just as *seen* like something *graspable*, with this or that grip. In other words, AIP and F5 neurons don’t respond to the visual stimuli itself but to the meaning that the object (e.g. cup) acquires according to the agent – and responding to a meaning is the same as “understanding” (21).

We agree with Marc Jeannerod and Pierre Jacob

in emphasizing the *pragmatic* nature of this understanding (22, 23). However, we are not so persuaded by their reformulation of the functional distinction between ventral and dorsal pathways prospected by Milner and Goodale’s model in terms of the opposition between a *semantic* and *pragmatic* processing of visual information. According to Jeannerod and Jacob, the “semantic” processing of visual information would be “the process whereby visual inputs are transformed in perceptual representations [...] whose pictorial non-conceptual contents must ultimately match the conceptual contents of beliefs”, and the “pragmatic” one would process visuomotor representations “for providing motor intentions with visual information about targets of action” (23).

In this way, however, Jeannerod and Jacob end up presupposing a stereotypical view of perception reducing the perception itself to a mere iconic description of the object. In addition, they assume a restrictive conception of action potentialities underestimating the role of the action itself in giving the objects we perceive their own meaning. It is not enough, as Jeannerod and Jacob hold, maintaining that in “planning and execution of more complex actions involving the use of tools, the distinction between action and perception loses much of its significance” (23). Indeed, it is necessary to rethink the distinction between action and perception not only from the “top”, i.e. from the so called “higher level motor representations”, but just beginning from the “bottom”, i.e. from the “lower level motor representations” requested for more simple visual guided actions, such as grasping any kind of object. As we said before, AIP and F5 neurons do not control only the execution of the action, but they allow also to code objects in terms of their possible interactions to the living and acting body of the subject. These possible interactions are directly perceived by the agent, and it is by their dynamic relations with the agent that objects acquire their own “meaningful value” (24).

Perceiving and understanding actions

The view that the ventro-dorsal pathway has both motor and perceptive functions has been further confirmed by the discovery of a new kind of sensori-

motor neurons in the ventral premotor cortex (F5) and in the rostral part of the inferior parietal lobe (PF and PG area) of monkeys: *mirror neurons* (25-29). Concerning *motor* properties, mirror neurons are similar to other F5 neurons quoted before: like these neurons, they code specific motor acts and not single movements. But everything changes about *visual* properties. Indeed, mirror neurons do not respond during the observation of an object. Rather, they fire *both* when the monkey performs a given action (such as picking up a nut) *and* when it sees someone (another monkey or the experimenter) performing a similar action.

Motor and visual responses of mirror neurons show different degrees of congruency. There are mirror neurons (more or less 30%) which discharge only if the observed action is just the same motor action they code. For the remaining mirror neurons, the congruency is broader. Some neurons respond during the execution of only one action (e.g. grasping) and during the observation of two actions (e.g. grasping and holding). Other neurons code only one executed and observed action, but with a different kind of selectivity (e.g. the execution of a precision grip and the observation of a precision grip or of a whole hand prehension). Finally, other neurons respond to the observation of a given action (e.g. the experimenter placing a piece of food on a tray) but they discharge when the agent performs another action (e.g. grasping that piece of food) that seems “logically” related to the first one.

The motor and visual properties of mirror neurons suggest that their characterizing mechanism directly matches the visual content of an action and its corresponding motor execution (30). Such a mechanism allows the observer to automatically translate the visual aspects of an observed action into that “vocabulary” of acts which, as we pointed out before, underlies the capability of acting of the observer itself. In other words, by mirror mechanism, the observer perceives the observed action in terms of one of the actions that belong to her/his own motor knowledge.

But what is the mirror mechanism for? A comparison between mirror neurons and other neurons located in a rostral region of the superior temporal sulcus (STS) let us realize that actually such a mechanism plays a fundamental role in understanding the meaning of actions performed by others (30). More than

fifteen years ago, David I. Perrett and his collaborators found in a rostral region of STS neurons discharging when the monkey observes biological actions (31, 32). A small set of them code actions (such as grasping, etc.) similar to those coded by mirror neurons. Contrary to mirror neurons, however, STS neurons do not respond to the execution of the actions they visually code. It shows that, although their visual responses are highly selective—allowing the observer to identify specific motor acts—, STS neurons are devoid of that mechanism of “directly matching” typical of mirror neurons.

This mechanism is the one that converts the *visual* representation of observed actions into a potential *motor* representation of the same actions. As *motor* neurons, mirror neurons also control the execution of the actions they code. It is well known that the control of the execution of an action (e.g. grasping an object) determines a relationship between the activation of involved neurons and the corresponding motor effects. The successful controlling and executing produce a basic motor knowledge concerning the meaning of actions coded by involved neurons. And this motor knowledge is useful *both* during further executions of these actions *and* also during the observation of the same actions performed by other individuals.

Without such a basic knowledge the observer would have just a visual information about biological movements done by others. But in order to understand the meaning of what is going on in front of him, the observer is required to have something more than a mere representation of the several visual features of the scene. Indeed, the mirror neuron activation shows how recognizing and understanding actions performed by others involve the same motor knowledge that the observer needs for controlling the execution of his own acting.

Some recent experiments corroborated the crucial role played by the motor knowledge in processing of sensorial information for recognizing actions. Maria Alessandra Umiltà and colleagues (33) showed that several F5 mirror neurons discharged both when the monkey saw the whole action performed by the experimenter and also when it could see only the beginning of the observed action, because the final phase (i.e. the specific hand-object interaction) was hidden

from view by a screen. The monkey was able to recognize the action even when the visual information about it was not complete, and that's why the potential motor representation evoked by mirror neuron discharging let the monkey integrate the information about the hidden phase of the observed scene and then understand the meaning of the action at all. In addition, Evelyne Kohler and colleagues (34) showed that a certain percentage of F5 mirror neurons respond both when the monkey observes a noisy action (e.g. breaking a nut) and also when the animal just hears the noise of the action, without seeing it. Even if sensorial information was different, the potential motor representation evoked was once more the same. This means that visual features of the observed action are coded just to let the monkey understand it: but if such a understanding is possible even by other sensorial inputs (e.g. sound ones), mirror neurons are able to code the action performed by the experimenter even in absence of *any* visual stimulus.

Several neurophysiological experiments (35-42) and brain imaging studies (43-50) demonstrated that a mirror neuron system does exist also in human beings. Such a system has a richer range of properties than the monkey one, and it has been suggested to underlie the human capabilities of imitation (51-54) and gestural communication, playing a key-role also in the evolution of language (55-60). Anyway, as well as in monkey, in humans beings too, the primary function of mirror neurons is to allow the observer to understand an action done by another individual. And by "understand" we mean the ability of the observer in recognizing the meaning of observed action just on the basis of her/his motor repertoire and immediate combination between perceiving and acting, without resorting to any kind of inference or reasoning.

In everyday life experience we usually attribute beliefs, intentions, motivations, desires, etc. to other agents. Most of our social behaviour depends on our capability to "read" into the other minds. But these "intentional stances", as Daniel C. Dennett (61) would say, belong to our cognitive and linguistic repertoire, and they presuppose the kind of "understanding" that only mirror neurons can provide with us. Indeed, just mirror neurons allow us to perceive the motor behaviour of other individuals and understand

its meaning through the motor knowledge which our own acting capability depends on.

Perception as an invitation to act

The analysis of cortical circuits coding acts (such as grasping) and the study of mirror neurons show how the processing of sensorial information by the ventro-dorsal pathway can't be reduced to a mere motor control, but implies a close relationship between action and perception. The meaning both of a perceived object and of an observed action is not confined to their visual features, but it arises from the *potential actions* evoked in the observer by the sight of *that* object or of *that* action. In this way, the observer is *at the same time* a perceiving and a (potentially) acting subject. The perception involves a (potential) motor engagement by the subject. Without this engagement the meaning would be relegated to the visual or pictorial description of the seen object and of the observed action. But such pictorial description is not enough for the subject to really understand what he is perceiving – an object or even more an action as well.

Thus, the researches concerning the cortical visual and motor systems make us dismantle the rigid and consolidated distinction between perception and action. From this point of view it would be worth the effort for neuroscientists themselves to deeply rethink some of the most significant philosophical perspectives on these issues: e.g. from Ernst Mach to Jules-Henri Poincaré about the motor character of perception; from Edmund Husserl to Maurice Merleau-Ponty about the role played by the acting body (*Leib*) in the dynamics of perception; and also from the most brilliant versions of Irish *ideaism* (for this term see 62) to American pragmatism.

It is well-known the George Berkeley's adage: "*esse est percipi et percipere*". Its meaning is not simply a declaration of idealism. Several passages in his works (63) show how Berkeley did not trust any pictorial theory of perception, refusing any reduction of the perception itself to a mere passive process. We like to think that the Bishop of Cloyne could agree with this notion of *perception in action* – on condition that this concept has to be interpreted as George Herbert

Mead later did. According to Mead, actually, not only “a perception has in it [...] all the elements of an act”, but also every perceived object (things and other people’s behaviour as well) “invites us to action with reference to it” (64). This “invitation to action” belongs to the content of our perceptual experience: it is thanks to such “invitation” that the surrounding objects and the actions performed by others come to acquire their own meaning for us.

References

1. Hurley SR. *Consciousness in Action*. Harvard, Harvard University Press, 1998.
2. Hurley SR. Perception and Action. *Synthese* 2001; 129: 3-40.
3. Ungerleider LG, Mishkin M. Two cortical visual systems. In Ingle DJ, Goodale MA, Mansfield RJW, eds: *Analysis of Visual Behaviour*. MIT Press, Cambridge (Mass.), 1982.
4. Milner AD, Goodale M. *The Visual Brain in Action*, Oxford University Press, Oxford, 1995.
5. Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, Acuna C. Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. *J Neurophysiol* 1975; 38: 871-908.
6. Rizzolatti G, Matelli M. Two different streams form the dorsal visual system: anatomy and functions. *Exp Brain Res* 2003; 153: 146-57.
7. Sakata H, Taira M, Murata A, Mine S. Neural mechanism of visual guidance of hand action in the parietal cortex of the monkey. *Cereb Cortex* 1995; 5: 429-38.
8. Matelli M, Luppino G, Rizzolatti G. Architecture of superior and mesial area 6 and of the adjacent cingulate cortex. *J Comp Neurol* 1991; 311: 445-62.
9. Matelli M, Luppino G. Functional anatomy of human motor cortical areas. In Boller F, Grafman J, eds: *Handbook of Neurophysiology*, vol. 11, Elsevier Science, Amsterdam, 1997.
10. Gentilucci M, Fogassi L, Luppino G, Matelli M, Camarda R, Rizzolatti G. Functional organization of inferior area 6 in the macaque monkey. I. Somatotopy and the control of proximal movements. *Exp Brain Res* 1988; 71: 475-90.
11. Rizzolatti G, Camarda R, Fogassi L, Gentilucci M, Luppino G, Matelli M. Functional organization of area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp Brain Res* 1988; 71: 491-507.
12. Murata A, Fadiga L, Fogassi L, Gallese V, Raos V, Rizzolatti G. Object representation in the ventral premotor cortex (Area F 5) of the monkey. *J Neurophysiol* 1997; 78: 2226-30.
13. Jeannerod M. The formation of the finger grip during prehension. A cortically mediated visuomotor pattern. *Behav Brain Sc* 1986; 19: 99-116.
14. Jeannerod M. *The Neural and Behavioural Organization of Goal-directed Movements*. Oxford, Oxford University Press, 1988.
15. Jeannerod M, Arbib MA, Rizzolatti G, Sakata H. Grasping objects: the cortical mechanism of visuomotor transformation. *Trends Neurosci* 1995; 18: 314-20.
16. Rizzolatti G, Fogassi L, Gallese V. Cortical mechanisms subserving object grasping and action recognition: a new view on the cortical motor functions. In Gazzaniga MS, ed: *The Cognitive Neurosciences*. MIT Press, Cambridge (Mass) 2000.
17. Rizzolatti G, Sinigaglia C. *So quel che fai. Il cervello che agisce e i neuroni specchio*. Milano, Raffaello Cortina, 2006.
18. Rizzolatti G, Gallese V. From action to meaning: a neurophysiological perspective. In Petit J-L, ed: *Les Neurosciences et la Philosophie de l'Action*. Vrin, Paris, 1997: 217-29.
19. Fadiga L, Fogassi L, Gallese V, Rizzolatti G. Visuomotor neurons: ambiguity of the discharge or ‘motor’ perception. *Inter J Psychophysiol* 2000; 35: 165-77.
20. Gibson J. *The Ecological Approach to Visual Perception*. Boston, Houghton Mifflin Company, 1979.
21. Petit J-L. Constitution by movement: Husserl in the light of recent neurobiological findings. In Petitot J, Varela FJ, Pachoud B, Roy J-M, eds: *Naturalizing Phenomenology: Issues in Contemporary Phenomenology and Cognitive Science*, Stanford University Press, Stanford, 1999: 220-44.
22. Jacob P, Jeannerod M. *Ways of Seeing. The Scope and Limits of Visual Cognition*. New York, Oxford University Press, 2003.
23. Jeannerod M, Jacob P. Visual cognition: a new look at the two-visuomotor systems model. *Neuropsychologia* 2005; 43: 301-12.
24. Gallese V. The inner sense of action. Agency and motor representation. *J Consciousness Studies* 2000; 7: 23-40.
25. Di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G. Understanding motor events: a neurophysiological study. *Exp Brain Res* 1992; 91: 176-80.
26. Rizzolatti G, Fadiga L, Gallese V, Fogassi L. Premotor cortex and the recognition of motor actions. *Cogn Brain Res* 1996; 3: 131-41.
27. Gallese V, Fadiga L, Fogassi L, Rizzolatti G. Action recognition in the premotor cortex. *Brain* 1996; 119: 593-609.
28. Fogassi L, Gallese V, Fadiga L, Rizzolatti G. Neurons responding to the sight of goal-directed hand/arm actions in the parietal area PF (7b) of the macaque monkey. *Soc Neurosci* 1998; 24: 654 (Abstract).
29. Gallese V, Fogassi L, Fadiga L, Rizzolatti G. Action representation and the inferior parietal lobule. In Prinz W, Hommel B, eds: *Attention and Performance XIX: Common Mechanisms in Perception and Action*. Oxford University Press, Oxford 2002: 335-355.
30. Rizzolatti G, Fogassi L, Gallese V. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci* 2001; 2: 661-70.
31. Perrett DI, Harries MH, Bevan R, et al. Frameworks of

- analysis for the neural representation of animate objects and actions. *J Exp Biol* 1989; 146: 87-113.
32. Perrett DI, Mistlin AJ, Harries MH, Chitty AJ. Understanding the visual appearance and consequence of hand actions. In Goodale MA, ed: *Vision and Action: the Control of Grasping*. Ablex, Norwood (NJ), 1990: 163-80.
 33. Umiltà MA, Kohler E, Gallese V, et al. I know what you are doing: A neurophysiological study. *Neuron* 2001; 32: 91-101.
 34. Kohler E, Keysers C, Umiltà MA, Fogassi L, Gallese V, Rizzolatti G. Hearing sounds, understanding actions: action representation in mirror neurons. *Science* 2002; 297: 846-8.
 35. Fadiga L, Fogassi L, Pavesi G, Rizzolatti G. Motor facilitation during action observation: a magnetic stimulation study. *J Neurophysiol* 1995, 73: 2608-11.
 36. Cochin S, Barthelemy C, Lejeune B, Roux S, Martineau J. Perception of motion and qEEG activity in human adults. *Electroencephalogr Clin Neurophysiol* 1998; 107: 287-95.
 37. Cochin S, Barthelemy B, Roux S, Martineau J. Observation and execution of movement: similarities demonstrated by quantified electroencephalography. *Eur J Neurosci* 1999; 11: 1839-42.
 38. Altschuler EL, Vankov A, Wang V, Ramachandran VS, Pineda JA. Person see, person do: human cortical electrophysiological correlates of monkey see monkey do cell. *Soc Neurosci* 1997; 719: 17 (Abstract).
 39. Altschuler EL, Vankov A, Hubbard EM, Roberts E, Ramachandran VS, Pineda JA. Mu wave blocking by observation of movement and its possible use as a tool to study theory of other minds. *Soc Neurosci* 2000; 68: 1 (Abstract).
 40. Hari R, Forss N, Avikainen S, Kirveskari S, Salenius S, Rizzolatti G. Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proc Natl Acad Sci USA* 1998; 95: 15061-5.
 41. Gangitano M, Mottaghy FM, Pascual-Leone A. Phase specific modulation of cortical motor output during movement observation. *NeuroReport* 2001; 12: 1489-92.
 42. Maeda F, Kleiner-Fisman G, Pascual-Leone A. Motor facilitation while observing hand actions: specificity of the effect and role of observer's orientation. *J Neurophysiol* 2002; 87: 1329-35.
 43. Rizzolatti G, Fogassi L, Matelli M, et al. Localization of grasp representations in humans by PET. *Exp Brain Res* 1996; 111: 246-52.
 44. Grèzes J, Costes N, Decety J. Top-down effect of strategy on the perception of human biological motion: a PET investigation. *Cogn Neuropsychol* 1998; 15: 553-82.
 45. Nishitani N, Hari R. Temporal dynamics of cortical representation for action. *Proc Natl Acad Sci USA* 2000; 97: 913-8.
 46. Grèzes J, Decety J. Functional anatomy of execution, mental simulation, observation and verb generation of actions: a meta-analysis. *Hum Brain Mapp* 2001; 12: 1-19.
 47. Buccino G, Binkofski F, Fink GR, et al. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci* 2001; 13: 400-4.
 48. Nishitani N, Hari R. Viewing lip forms: cortical dynamics. *Neuron* 2002; 36: 1211-20.
 49. Grèzes J, Armony JL, Rowe J, Passingham RE. Activations related to 'mirror' and 'canonical' neurons in the human brain: an fMRI study. *Neuroimage* 2003; 18: 928-37.
 50. Buccino G, Lui F, Canessa N, et al. Neural circuits involved in the recognition of actions performed by non con-specifics: an fMRI study. *J Cogn Neurosci* 2004; 16: 114-26.
 51. Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G. Cortical mechanisms of human imitation. *Science* 1999; 286: 2526-8.
 52. Iacoboni M, Koski LM, Brass M, et al. Reafferent copies of imitated actions in the right superior temporal cortex. *Proc Natl Acad Sci USA* 2001; 98: 13995-9.
 53. Rizzolatti G, Fadiga L, Fogassi L, Gallese V. From mirror neurons to imitation: facts and speculations. In Meltzoff AN, Prinz W, eds: *The Imitative Mind. Development, Evolution, and Brain Bases*. Cambridge University Press, Cambridge (Mass.), 2002: 247-66.
 54. Buccino G, Vogt S, Ritzl A, et al: Neural circuits underlying imitation learning of hand actions: an event-related fMRI study. *Neuron* 2004; 42: 323-34.
 55. Rizzolatti G, Arbib MA. Language within our grasp. *Trends Neurosci* 1998; 21: 188-94.
 56. Gentilucci M, Benuzzi F, Gangitano M, Grimaldi S. Grasp with hand and mouth: a kinematic study on healthy subjects. *J Neurophysiol* 2001; 86: 1685-99.
 57. Fadiga L, Craighero L, Buccino G, Rizzolatti G. Speech listening specifically modulates the excitability of tongue muscles: a TMS study. *Eur J Neurosci* 2002; 17: 1703-14.
 58. Gentilucci M. Grasp observation influences speech production. *Eur J Neurosci* 2003; 17: 179-84.
 59. Rizzolatti G, Craighero L. The mirror neuron system. *Ann Rev Neurosci* 2004; 27: 169-92.
 60. Rizzolatti G, Buccino G. The mirror neuron system and its role in imitation and language. In Dehaene S, Duhamel J-R, Hauser MD, Rizzolatti G, eds: *From Monkey Brain to Human Brain. A Fyssen Foundation Symposium*. MIT, Cambridge (Mass.), 2005: 213-33.
 61. Dennett D. *The Intentional Stance*. Cambridge (Mass.), MIT Press, 1987.
 62. Musgrave A. *Common Sense, Science and Scepticism. A Historical Introduction to the Theory of Knowledge*. Cambridge, Cambridge University Press, 1993.
 63. Luce AA, Jessop TE. *The Works of George Berkeley Bishop of Cloyne*. London, Nelson and Sons, 1948-1957.
 64. Morris CW, Brewster JM, Dunham AM, Miller D. Mead GH, *The Philosophy of the Act*. Chicago, University of Chicago, 1938.

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