



## The “Conscious” Dorsal Stream: Embodied Simulation and its Role in Space and Action Conscious Awareness

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**Abstract:** The aim of the present article is three-fold. First, it aims to show that perception requires action. This is most evident for some types of visual percept (e.g. space perception and action perception). Second, it aims to show that the distinction of the cortical visual processing into two streams is insufficient and leads to possible misunderstandings on the true nature of perceptual processes. Third, it aims to show that the dorsal stream is not only responsible for the unconscious control of action, but also for the conscious awareness of space and action.

### 1. Introduction

Perception and action have been traditionally considered separate domains, each of them being implemented in separate anatomical and functional brain sectors. According to this “classic” view, individuals first perceive and then act. In primates, the paradigmatic sensory modality for the study of the mechanisms underlying perception is vision. Visual information is processed both serially and along parallel pathways. Serial organization fits well with the classical concept that information travels from the periphery to progressively more complex “association” areas where perception occurs and then proceeds to output channels for action. In contrast, the parallel organization of visual processes needs explanation.

A particularly influential account of why there is parallel processing of visual information in the primate visual cortex is that proposed by Ungerleider and Mishkin (1982). According to these authors, the visual cortical areas are organized in two separate

streams of visual information. A dorsal stream, which includes visual areas MT, MST, FST, V3A, and V6, and culminates in the inferior parietal lobule, and a ventral stream, which includes visual areas V3 and V4, and culminates in the inferior temporal cortex. The dorsal stream is responsible for perception of space, while the ventral stream for object perception.

An equally influential and radically different view was advanced by Milner and Goodale (Goodale and Milner 1992; Milner and Goodale 1995). In accord with Mishkin and Ungerleider (1982) they maintain that there is a fundamental functional difference between the dorsal and ventral stream. They deny, however, that the difference is in the resulting percept (space vs. object). According to Goodale and Milner the difference is in the output characteristics of the two cortical visual streams. The ventral stream is fundamental for perception. The dorsal stream, in contrast, processes visual stimuli to provide high order visual information for the control of action, but it is not involved in perception.

A similar view was independently proposed by Marc Jeannerod (1994, 1997). According to Jeannerod, the ventral stream is responsible for the “semantic mode” of object representation, while the dorsal stream is responsible for the “pragmatic mode” of stimulus processing. The semantic mode of object representation refers to object analysis described in object-centered coordinates. The pragmatic mode indicates the type of processing that stimuli have to undergo for action organization. Although the distinction between a semantic and a pragmatic system proposed by Jeannerod appears to be more cautious than that of Milner and Goodale, the essence of the two proposals is very similar.

This view was recently reissued by Mel Goodale as follows:

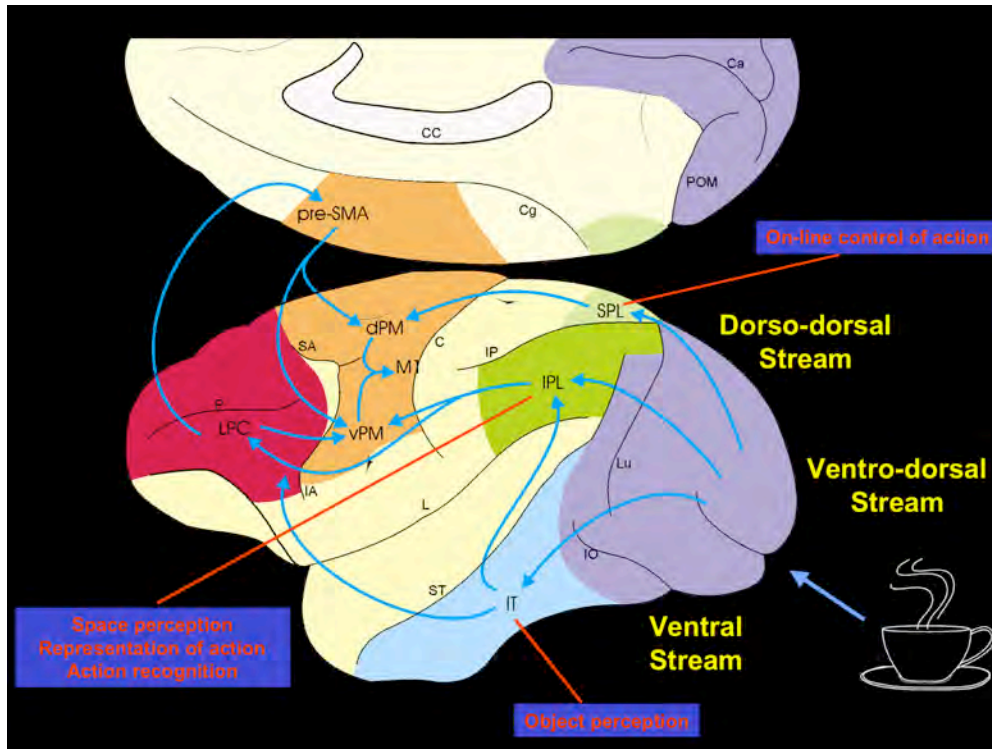
According to this account, the ventral stream transforms visual information into perceptual representations, forming the visual foundation for our cognitive life, allowing us to recognize objects and understand their causal relations, to communicate with others about the world beyond our bodies, and to identify goals and plan actions with respect to those goals. In contrast, the dorsal stream which utilizes moment-to-moment information about the disposition of objects within egocentric frames of reference, mediates the control of those goal-directed acts (Goodale 2005, p. 328).

The problem is that several empirical results can hardly be reconciled with this rigid and dichotomous view.

The aim of the present article is three-fold. First, it aims to show that perception—or at least *some kind of perception*—requires action. This is most evident for some types of visual percept (e.g. space perception and action perception). Second, it aims to show that the distinction of the cortical visual processing into two streams is insufficient and leads to possible misunderstandings on the true nature of perceptual processes. Third, it aims to show that the dorsal stream is not only responsible for the unconscious control of action, but also for the conscious awareness of space and action.

I will briefly review empirical findings suggesting that visual processing is carried out along three distinct streams (see Figure 1). These three streams are qualified as dorso-

dorsal, ventro-dorsal and ventral streams (for a detailed analysis of the dorsal streams, see Rizzolatti and Matelli 2003; Rozzi *et al.* 2006).



**Figure 1: The three visual streams:** Lateral and mesial view of the macaque monkey brain showing the main connectivity along the dorso-dorsal, ventro-dorsal and ventral streams of visual processing and their hypothesized functions. Abbreviations: C=central sulcus; Ca=calcarine fissure; CC=corpus callosum; cg=cingulate gyrus; dPM=dorsal premotor cortex; IA=inferior arcuate sulcus; IO=inferior orbital sulcus; IP=inferior parietal lobule; IT=inferior temporal cortex; L=lateral fissure; LPC=lateral prefrontal cortex; Lu=lunate sulcus; MI=primary motor cortex; P=principal sulcus; pre-SMA=pre-supplementary motor area; SPL=superior parietal lobule; ST=superior temporal sulcus.

The dorso-dorsal stream has the characteristics suggested by Milner, Goodale and Jeannerod when they describe the dorsal stream as a whole. It appears to be possibly the only stream that is not directly related to perception. The ventro-dorsal stream, which will be the main focus of this article, is responsible for the organization of actions directed towards objects, but also for space and action perception and conscious awareness. Finally, the ventral stream is responsible for the organization of actions following object categorization, and for object semantics. All three visual streams terminate into frontal cortical areas endowed with different degrees of complexity.

## 2. The dorsal streams

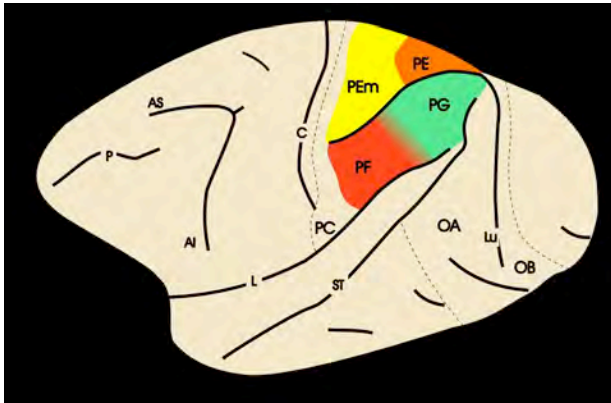
The intraparietal sulcus is, evolutionary speaking, a very ancient sulcus. This sulcus is already present in prosimians and represents a fundamental parietal landmark. It subdivides the posterior parietal lobe into two main sectors: the superior parietal lobule (SPL) and the inferior parietal lobule (IPL). These two sectors receive different cortical inputs and have different connections with the motor cortex and frontal lobe. Early experiments in monkeys showed that the superior parietal lobule (SPL) is part of the somatosensory system. It receives information from the primary sensory cortex, and in particular from those areas that code proprioception, and sends inputs to the primary motor cortex (area F1) and to the dorsal premotor cortex (area F2). Recent neurophysiological data showed that the SPL also receives visual inputs. Neurons activated by visual stimuli have been described in its caudal part (Galletti et al. 1996; Caminiti et al. 1996) and, in particular, in areas V6A and MIP. Both these areas are connected with frontal motor areas. Their main target is the dorsal premotor cortex (area F2) (Caminiti et al. 1996; Matelli et al. 1998).

Like SPL, also IPL (especially its rostral sector) receives somatosensory afferents. In addition, IPL is the main site of convergence of the pathways from the extrastriate visual areas of the dorsal stream. It projects to areas of the ventral premotor cortex (areas F4 and F5) and to the prefrontal lobe. The functional properties of IPL are in accord with the pattern of anatomical connections. IPL neurons are often bimodal responding both to visual and somatosensory stimuli (see also below). Taken together, these findings indicate that the parietal cortex performs two separate analysis of incoming sensory information. The analysis carried out in SPL (dorso-dorsal stream) concerns mostly proprioceptive input, but with an important visual contribution. The analysis performed in IPL (ventro-dorsal stream) consists in the integration of visual, auditory and somatosensory stimuli for action on and perception of the external world.

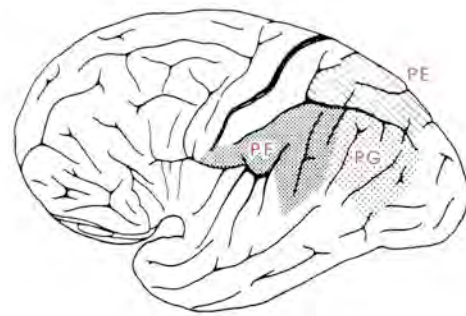
Before reviewing the organization of the ventro-dorsal stream in detail, an important point about the homology between human and other primates parietal lobe organization should be clarified. Human posterior parietal lobe as that of the macaque monkey is formed by two lobules—SPL and IPL—separated by the intraparietal sulcus. As shown by Forster (1936), contrary to the original parcellation of Brodmann, SPL is basically co-extensive with area 5 (5a + 5b), while IPL with area 7 (7a + 7b).

This means that the cytoarchitectonic organization of the posterior parietal lobe is similar in monkeys and humans. This view was confirmed by von Bonin and Bailey (1947) who, adopting the terminology of von Economo (1929), found that in monkeys as in humans SPL is formed in large part by area PE (area 5) and the IPL by areas PF (7b) and PG (7a). Thus, when monkey data on area 7 are used to discuss functional properties of human parietal lobe, they should be used in reference to human IPL and not SPL as one can be tempted to do on the basis of the (wrong) Brodmann map. Similarly, the data on monkey area 5 should be used in reference to human SPL.

A



B



**Figure 2: The inferior parietal lobule: monkey-human homology.** **A.** Lateral view of the macaque monkey brain showing the cytoarchitectonic parcellation of the superior and inferior parietal lobules according to Von Bonin and Bailey (1947). **B.** Lateral view of the human brain showing the cytoarchitectonic parcellation of the superior and inferior parietal lobules according to Von Economo (1929).

In the following sections I describe in detail two parallel parietal-premotor neural circuits, both components of the ventro-dorsal stream: the VIP-F4 network and the PF/PFG-F5 network. It will be shown that these networks are involved in the organization of action in space and space awareness and in action understanding and awareness, respectively.

### 3. The ventro-dorsal stream: action in space perception

The cortical circuit formed by area F4, which occupies the posterior sector of the ventral premotor cortex of the macaque monkey, and area VIP (Colby *et al.* 1993), which occupies the fundus of the intraparietal sulcus, is involved in the *organization of head and arm actions in space*. Single neuron studies showed that in area VIP there are two main classes of neurons responding to sensory stimuli: purely visual neurons and bimodal, visual and tactile neurons (Colby *et al.* 1993). Bimodal VIP neurons respond independently to both visual and tactile stimuli. Tactile receptive fields are located predominantly on the face. Tactile and visual receptive fields are usually in “register,” that is, the visual receptive field encompasses a three-dimensional spatial region (peri-personal space) around the tactile receptive field. Some bimodal neurons are activated preferentially or even exclusively when 3D objects are moved towards or away from the tactile receptive field. About thirty percent of VIP neurons code space in reference to the monkey’s body. There are also neurons that have hybrid receptive fields. These receptive fields change position when the eyes move along a certain axis, but remain fixed when the eyes move along another axis (Duhamel *et al.* 1997).

Consistent with the single neuron data, are the results of lesion studies (Duhamel, personal communication). Selective electrolytic lesion of area VIP in monkeys

determines mild but consistent contralesional neglect for peri-personal space. No changes were observed in ocular saccades, pursuit and optokinetic nystagmus. Tactile stimuli applied to the contralesional side of the face also failed to elicit orienting responses.

Single neurons studies showed that most F4 neurons discharge in association with monkey's active movements (Gentilucci *et al.* 1988). The movements more represented are head and arm movements, such as head turns and reaching. Most F4 neurons respond to sensory stimuli. As neurons in VIP, F4 sensory-driven neurons can be subdivided into two classes: unimodal, purely sensory neurons, and bimodal, somatosensory and visual neurons (Gentilucci *et al.* 1988; Fogassi *et al.* 1992, 1996). Tactile receptive fields, typically large, are located on the face, chest, arm and hand. Visual receptive fields are also large. They are located in register with the tactile ones, and similarly to VIP, confined to the peri-personal space (Gentilucci *et al.* 1983, 1988; Fogassi *et al.* 1992, 1996; Graziano *et al.* 1994). Recently, trimodal neurons responding also to auditory stimuli were described in F4 (Graziano *et al.* 1999).

Several electrophysiological studies have shown that in most F4 neurons visual receptive fields do not change position with respect to the observer's body when the eyes move (Gentilucci *et al.* 1983; Fogassi *et al.* 1992, 1996; Graziano *et al.* 1994). The visual responses of F4 neurons do not signal positions on the retina, but positions in space relative to the observer. The spatial coordinates of the visual receptive fields are anchored to different body parts, and not to a single reference point, and they are coded in egocentric coordinates (Fogassi *et al.* 1996 a,b). Furthermore, visual receptive fields located around a certain body part (e.g., the arm) move when that body part is moved (Graziano *et al.* 1997).

Empirical evidence in favor of the embodied simulation-based motor nature of space coding derives from the properties of F4 neurons. In principle there are two main possibilities on what these neurons code. The first is that they code space "visually". If this is so, given a reference point the neurons should signal the location of objects by using a Cartesian or some other geometrical system. The alternative possibility is that the discharge of neurons reflects a potential, simulated motor action directed towards a particular spatial location. This simulated potential action would create a motor space. When a visual stimulus is presented, it evokes directly the simulation of the congruent motor schema which, regardless of whether the action is executed or not, maps the stimulus position in motor terms.

Arguments in favor of the visual hypothesis are the tight temporal link between stimulus presentation and the onset of neural discharge, the response constancy, and the presence of what appears to be a visual receptive field. If, however, there is a strict association between motor actions and stimuli that elicit them, it is not surprising that stimulus presentation determines the effects just described. More direct evidence in favor of a motor space came from the study of properties of F4 neurons in response to moving stimuli. According to the visual hypothesis, each set of neurons, when activated should specify the object location in space, regardless of the stimulation's temporal dimension. A locus 15 cm from the tactile origin of the visual receptive field should remain 15 cm from it regardless of *how* the object reaches this position. The spatial map, as expressed by receptive field organization, should be basically static. In contrast, in the case of motor space, because time is inherent to movement, the spatial map may have dynamic

properties and may vary according to the change in time of the object's spatial location. The experiments of Fogassi et al. (1996) showed that this is indeed the case. The visual receptive field extension of F4 neurons increases in depth when the speed of an approaching stimulus increases.

#### 4. The ventro-dorsal stream: action in spatial conscious awareness

The notion that spatial awareness is linked to movement is pretty old. Von Helmholtz (1896) proposed the notion that the “a-priori” nature of our representation of space depends on the fact that it is generated by active exploratory behavior. Indeed, as it has been argued elsewhere (see Rizzolatti *et al.* 1997), a strong support to the notion that spatial awareness derives from motor activity is the demonstration of the existence of peri-personal space. From a purely sensory point of view, there is no principled reason why our eyes should select light stimuli coming exclusively from a space sector located around our body. Light stimuli arriving from far or from near should be equally effective. However, if we consider that peri-personal stimuli occupy the space where the targets of the actions performed by hands and mouth are mostly located, it becomes clear why space is mapped in motor terms.

It is perhaps worth emphasizing the closeness of the view emerging from neuroscience, and the philosophical perspective offered by phenomenological philosophers on space perception (see also Zahavi 2002). As Merleau-Ponty (1962, p. 243) wrote, space is "...not a sort of ether in which all things float.... The points in space mark, in our vicinity, the varying range of our aims and our gestures." Furthermore, it is interesting to note that Husserl wrote that every thing we see, we simultaneously also see it as a tactile object, as something which is directly related to the lived body, but not by virtue of its visibility (Husserl 1989). The body entertains a dual reality of spatial externality and internal subjectivity. The perspectival spatial location of our body provides the essential foundation to our determination of reality. But in contrast to what Husserl considered the *physiological* definition of the body—by considering it a material object, the Körper—contemporary neurophysiological research suggests that a part of the body, the sensory-motor system, is also responsible for the phenomenal awareness of the body's relations with the world.

Why is action important in spatial awareness? Because what integrates multiple sensory modalities within the F4-VIP neural circuit is action embodied simulation (Gallese 2005a,b, 2006). Vision, sound and action are parts of an integrated system; the sight of an object at a given location, or the sound it produces, automatically triggers a “plan” for a specific action directed toward that location. What is a “plan” to act? It is a simulated potential action.

The characterization so far provided of this cortical network would seem at first sight to be fully consistent with the control of body actions within peri-personal space. If, however, we consider the results of lesion of this network, a different picture emerges. Unilateral lesion of the ventral premotor cortex of the monkey, including area F4, produces two different series of deficits: motor deficits and perceptual deficits (Rizzolatti *et al.* 1983; see also Rizzolatti *et al.* 2000). Motor deficits consist in a reluctance to use the contralesional arm, spontaneously or in response to tactile and visual stimuli, and in a failure to grasp with the mouth food presented contralateral to the side of the lesion.

Perceptual deficits concern neglect of the contralesional peripersonal space, and of the personal (tactile) space. A piece of food moved in the contralesional space around the monkey's mouth does not elicit any behavioral reaction. Similarly, when the monkey is fixating a central stimulus, the introduction of food contralateral to the lesion is ignored. In contrast, stimuli presented outside the animal's reach (far extra-personal space) are immediately detected.

Neglect in humans occurs after lesion of the IPL and, less frequently, following damage of the frontal lobe, and in particular following lesions of area 6, 8, and 45 (see Bisiach and Vallar 2000). The most severe neglect in humans occurs after lesion of the right IPL. In the full-fledged unilateral neglect, patients may show a more or less complete deviation of the head and eyes towards the ipsilesional side. Routine neurological examination shows that patients with unilateral neglect typically fail to respond to visual stimuli presented in the contralesional half field and to tactile stimuli delivered to the contralesional limbs. As in monkeys, also in humans neglect may selectively affect the extrapersonal and the peripersonal space.

In humans, this dissociation was first described by Halligan and Marshall (1991). They examined a patient with severe neglect using a line bisection task. In this task the subject is usually required to mark the midpoint of a series of lines scattered all over a sheet of paper. The task was executed in the near space and in the space beyond hand reaching distance using a laser pen that the patient held in his right hand. The results showed that when the line was bisected in the near space the midpoint mark was displaced to the right, as typically occurs in neglect patients. However, the neglect dramatically improved or even disappeared when the testing was carried out in the far space. A similar dissociation was reported by Berti and Frassinetti (2000). Other authors described the opposite dissociation: severe deficits in tasks carried out in the extrapersonal space, slight or no deficit for tasks performed in the peripersonal space (see Shelton *et al.* 1990; Cowey *et al.* 1994, 1999). The lesions causing neglect in humans are usually very large, thus while the findings of separate systems for peripersonal and extrapersonal space are robust and convincing, any precise localization of the two systems in humans is at the moment impossible.

In conclusion, lesions of IPL and its frontal targets both in monkeys and humans determine body awareness deficits. Furthermore, it must be stressed that not only does IPL appear to play a fundamental role in body and spatial awareness, but it is also necessary for the *conscious awareness of the quality of objects* presented within peripersonal space. Evidence in favor of this point of view comes from a series of clinical and neuropsychological studies. Marshall and Halligan (1988) reported the case of a lady who, due to a severe visual neglect, explicitly denied any difference between the drawing of an intact house and that of the same house when burning, if the relevant features for the discrimination were on the neglected side. However, when forced to choose the house where she would prefer to live, she consistently choose the intact one, showing in this way an implicit knowledge of the content she was unable to report.

Berti and Rizzolatti (1992) confirmed these findings in a systematic way. In their experiments patients with severe unilateral neglect were asked to respond as fast as possible to target stimuli presented within the intact visual field by pressing one of two keys according to the category of the target (fruits and animals). Before showing these



stimuli, pictures of animals and fruits were presented to the neglected field as priming stimuli. The patients denied of seeing these priming stimuli. Yet, their responses to the stimuli shown in the intact field were facilitated by the primes. This occurred not only in “highly congruent conditions”, that is when the prime stimulus and the target were physically identical (e.g. a dog), but also when prime and stimulus constituted two elements of the same semantic category, though physically dissimilar (e.g. a dog and an elephant).

These findings demonstrate that neglect patients are able to process stimuli presented within the neglected field up to a categorical semantic level of representation. However, they are not aware of them in the absence of IPL processing. This implies that the parieto-premotor circuits of the ventro-dorsal stream must be intact for achieving awareness even of those stimuli, such as fruits or animals that are mostly analyzed in the ventral stream.

Lesions of sensory-motor circuits, whose primary function is that of controlling movements of the body or of body parts towards or away from objects, produce deficits that do not exclusively concern the capacity to orient towards objects or to act upon them. These lesions produce also deficits in body, space, and object awareness.

## **5. The ventro-dorsal stream: action understanding**

Our social world is inhabited by a multiplicity of acting individuals. Much of our social competence depends on our capacity for understanding the meaning of the actions we witness and of the intentions producing those actions. What makes our perception of actions different from our perception of the inanimate world is the fact that there is something shared between the first and third person perspective of actions; the observer and the observed are both human beings endowed with a similar brain-body system making them act alike (Gallese 2001). Even more importantly, the observer and the observed share the same action-related neural circuits. The discovery of mirror neurons in the ventral premotor cortex of the monkey has triggered new perspectives on the neural mechanisms at the basis of action understanding. This will be the focus of the next section.

## **6. The mirror neuron system for actions in monkeys and humans: empirical evidence**

More than a decade ago a new class of motor neurons was discovered in the ventral premotor cortex of the macaque monkey: mirror neurons. These neurons discharge not only when the monkey executes goal-related hand and/or mouth actions like grasping objects, but also when observing other individuals (monkeys or humans) executing similar actions (di Pellegrino *et al.* 1992; Gallese *et al.* 1996; Rizzolatti *et al.* 1996; Ferrari *et al.* 2003). Neurons with similar mirroring properties, matching action observation and execution have also been discovered in a sector of the posterior parietal cortex reciprocally connected with area F5 (see Rizzolatti *et al.* 2001; Gallese *et al.* 2002; Fogassi *et al.* 2005). It has been proposed that this “motor resonance” may underpin a direct form of action understanding (Gallese *et al.* 1996; Rizzolatti *et al.* 1996; Rizzolatti *et al.* 2001; Gallese *et al.* 2004; Rizzolatti and Craighero 2004), by exploiting embodied

simulation, a specific mechanism by means of which the brain/body system models its interactions with the world (Gallese 2001, 2003a, b, 2005a, b, 2006).

A series of experiments by Umiltà *et al.* (2001) showed that F5 mirror neurons become active also during the observation of partially hidden actions, when the monkey can predict the action outcome, even in the absence of the complete visual information about it (Umiltà *et al.* 2001). Macaque monkey's mirror neurons therefore represent actions made by others not exclusively on the basis of their visual description, but also on the basis of the anticipation of the final goal of the action, by means of the activation of its motor representation in the observer's premotor cortex.

In another series of experiments it has been shown that a particular class of F5 mirror neurons ("audio-visual mirror neurons") respond not only when the monkey executes and observes a given hand action, but also when it just hears the sound typically produced by the action (Kohler 2002). These neurons respond to the sound of actions and discriminate between the sounds of different actions, but do not respond to other similarly interesting sounds such as arousing noises, or monkeys' and other animals' vocalizations. In sum, the different modes of presentation of events as intrinsically different as sounds, images, or willed acts of the body, are nevertheless bound together within a simpler level of semantic reference, underpinned by the same network of audio-visual mirror neurons. The presence of such neural mechanism within a non-linguistic species can be interpreted as the neural correlate of the dawning of a conceptualization mechanism (see Gallese 2003c; Gallese and Lakoff 2005).

Different experimental methodologies and techniques have demonstrated also in the human brain the existence of a mirror neuron system matching action perception and execution (for review, see Rizzolatti *et al.* 2001; Gallese 2003a, b, 2006; Rizzolatti and Craighero 2004; Gallese *et al.* 2004). During action observation there is a strong activation of premotor and parietal areas, the likely human homologue of the monkey areas in which mirror neurons were originally described. The mirror neuron matching system for actions in humans is somatotopically organized, with distinct cortical regions within the premotor and posterior parietal cortices being activated by the observation/execution of mouth, hand, and foot related actions (Buccino *et al.* 2001).

More recently, it has been shown that the mirror neuron system for actions in humans is directly involved in imitation (Iacoboni *et al.* 1999; Buccino *et al.* 2004a) and in the perception of communicative actions (Buccino *et al.* 2004b). Furthermore, the premotor cortex containing the mirror system for action is involved in processing action-related sentences (Hauk *et al.* 2004; Tettamanti *et al.* 2005; Buccino *et al.* 2005; see also Pulvermuller 2002).

A recent study by Buxbaum *et al.* (2005) on posterior parietal neurological patients with Ideomotor Apraxia has shown that they were not only disproportionately impaired in the imitation of transitive as compared to intransitive gestures, but they also showed a strong correlation between imitation deficits and the incapacity of recognizing observed goal-related meaningful hand actions. These results further corroborate the notion that the same action representations within the ventro-dorsal stream underpin both action production and action understanding.

## 7. The ventro-dorsal stream and action conscious awareness

The conscious awareness of action is one aspect of the broader issue of self-awareness. The latter, far from being a monolithic entity, appears to be a dynamic and constantly oscillating process, the ultimate results of a long developmental maturation process, starting from the very first months of age. According to Rochat (2003), this developmental maturation process unfolds during five different developmental stages, starting with the capacity of infants to discriminate stimulation originating from their own body from that produced by an external source. Self-awareness is completed around 5-6 years of age when children become capable of entertaining multiple representations and perspectives onto themselves as well as onto others. The results of the research of developmental psychology are illuminating because they show that from a very early start the sensory-motor system is implied in the building of a self-conscious self. Even more so when the issue of self-awareness is focused on the domain of action.

The problem of how the conscious awareness of acting and intending to act are mapped in the brain has been recently investigated with a variety of techniques in healthy controls as well as in neurological patients. This experimental approach is very important because it bypasses the preconceived philosophical arguments previously dominating this debate, leaving to empirical findings the burden of settling it. Several studies converge in showing that the premotor and the posterior parietal cortex are crucial in allowing individuals to be aware not only of when they act but also of when they intended to act (for review, see Haggard 2005). Haggard and Magno (1999) showed that transcranial magnetic stimulation (TMS) of the primary motor cortex delays reaction times of action performance while TMS of the pre-supplementary motor area (pre-SMA) delays reaction times of the *judgment* on when the action occurred. In an fMRI study on healthy participants Lau et al. (2004) showed increased activation of pre-SMA and of the cortex within the intraparietal sulcus when participants had to judge when they *intended to act* with respect to when they really performed the action.

The role of posterior parietal cortex in the awareness of self-generated finger movements was described by Sirigu et al. (1999) in a paper investigating three apraxic patients who suffered a left posterior parietal lesion. Sirigu et al. (1999) showed that apraxic patients were disproportionately worse than controls when asked to differentiate between their and the experimenter's gloved hand movements. These results are nicely complemented by those of MacDonald and Paus (2003) in a study carried out in healthy participants. Their results showed that the temporary inactivation of the posterior parietal cortex by means of repetitive TMS impaired the participants' assessment of asynchrony between their active—but not for passive—finger movements and those of a virtual hand they were looking at. Altogether these results are consistent for a role of posterior parietal cortex, a recipient of the dorsal stream, in evaluating the temporal congruency of peripheral (visual stimuli) and central (efference copy) signals associated with self-generated movements. As suggested by MacDonald and Paus (2003), this region may contribute to the sense of agency.

More recently Sirigu *et al.* (2004) showed that patients with parietal lesions could report when they started moving, but not when they first became aware of their intention to move. Even more striking are the results recently reported by Berti et al. (2005). This study assessed the anatomical distribution of lesions in right-brain-damaged hemiplegic

patients, who obstinately denied their motor impairment, claiming that they could move their paralyzed limbs. The results showed that the patients' anosognosia was associated with lesions in areas related to the programming of motor acts, particularly Brodmann's premotor areas 6 and 44, the primary motor cortex, and the somatosensory cortex. The premotor regions responsible for the control of action are also crucial for the agents' conscious awareness of the same actions. It appears therefore, as emphasized by Berti et al. (2005, p. 490) that conscious awareness is "neither the prerogative of some kind of central executive system, hierarchically superimposed on sensory-motor and cognitive functions, nor a function that is physiologically and anatomically separated from the primary process that has to be monitored".

The anatomical correlates of anosognosia for action show that conscious awareness is implemented in the same cortical network responsible for the process that has to be controlled. This is evident also from studies investigating the neural correlates of phantom limb experiences. There is evidence that congenitally limb deficient patients may develop phantom limb sensations (the so-called *aplastic phantoms*), despite the fact that they never moved these absent parts of their bodies (see Ramachandran 1993; Melzak *et al.* 1997; Ramachandran and Rogers-Ramachandran 1996; Ramachandran and Hirstein 1998). Brugger et al. (2000) described one of these cases. fMRI imaging of their patient during phantom limb sensations of hand movements showed no activation of primary sensorimotor areas, but of premotor and posterior parietal cortex. Aplanic phantoms can therefore be explained as the phenomenal correlate of planning action with an absent limb.

## 8. A new perspective on action, perception, and conscious awareness

How does our brain model our acting body? And how does it model the acting body of other individuals? What is the relevance of these bodily models/representations for our capacity to phenomenally experience space, our own acting body and the acting body of others? One way of dealing with these questions is by following the classic distinction introduced by Head and Holmes (1911) and Schilder (1935) between an *unconscious* body map—the body-schema—and the *conscious perception* of our own body, the body-image. This dichotomy, however, seems to presuppose a clear-cut division of labor between neural systems operating below and above the level of consciousness. As it should be now clear, this distinction appears to be over simplistic. The present article, by reviewing almost twenty years of neuroscientific research, aimed at providing new answers to these questions.

Perception can be accounted for only if one takes into consideration the relationship between the agent and his/her environment. Actions are fundamental for building a meaningful description of the visual world. Only through action visual experience can be "validated" and acquire a meaning for the individual. The influence of action on perception is—as we have seen—instantiated by space perception. The conventional view about space is that space is unitary, and that the brain has a center specifically devoted to space representation. According to this view, this center is used for all purposes, for walking, for reaching objects, or for describing a scene verbally. Classically, this putative multi-purpose center was considered to be located in the parietal lobe (Critchley 1953; Hyvärinen 1982; Ungerleider and Mishkin 1982). Language here

appears to play ontological tricks. Our language-based definitions do not necessarily translate into real entities in the brain. We have seen that space, although unitary when examined introspectively, is not represented in the brain as a single multipurpose map. Neuropsychological evidence indicates that lesions of dorsal stream recipient parieto-premotor circuits, whose primary function is that of controlling orienting movements, as well as movements of the body or of body parts towards objects within peripersonal space, produce deficits which do not exclusively concern the capacity to orient towards objects or to act upon them. These lesions also produce deficits in the conscious awareness of peripersonal space.

In the case of action understanding the issue is how to build a meaningful account of the action made by others when observed. It is obvious that there is a visual system that analyzes and describes in pictorial ways the actions of others. However, the view that such "pictorial" analysis is *per se sufficient* to provide an understanding of the observed action must be questioned. Without a reference on personal knowledge, this description is devoid of any meaning for the observing individual. This impasse can be solved if there is a system matching the observed action on an internal motor representation of the same action. The mirror system for actions has precisely the properties that such a system must have. It internally represents the action and it responds when another agent performs a similar action. According to this view, action understanding is viewed as an embodied simulation function. It relies on a neural circuit involved in the control of action.

Furthermore, this motor-centered view of perception allows one to explain a series of data on the effect of motor function on stimulus perception, which would be very difficult to account for according to the conventional view on perception. There is a large body of literature demonstrating motor effects on perception (for a review, see Viviani 2002). For reasons of space I will limit myself here to discuss only some psychological experiments more closely related to the points addressed above.

Craighero *et al.* (1999) demonstrated that preparation of a grasping movement affects detection and discrimination of a visual stimulus. In this experiment normal subjects were required to grasp a bar after the presentation of a visual stimulus whose orientation was either congruent or incongruent with that of the bar. The results showed that grasping preparation enhances the detection of a visual stimulus whose intrinsic properties are congruent with those of the object to be grasped. The role played by handedness in performing perceptual tasks is another example of the involvement of motor processes in perceptual functions. De Sperati and Stucchi (1997) showed that right- and left-handed normal subjects used an internal simulation of the movement of their dominant hand in order to discriminate between observed screwing and unscrewing screwdrivers. In another series of experiments Gentilucci *et al.* (1998a, b), asked normal subjects to judge the handedness of pictures of hands and fingers assuming different postures. The results showed that the presentation of postures that hand and fingers commonly assume at rest, or when interacting with objects, facilitated the responses with respect to the presentation of less usual hand-finger postures, even when the latter were richer in visual cues useful for handedness recognition (see also Parsons 1987, 1994 and Parsons *et al.* 1995 for similar results). Once again motor knowledge was employed to solve a perceptual task.

The data reviewed here show that different and parallel parieto-premotor networks, recipient of visual information processed within one part of the dorsal stream, create internal representations of actions. These representations may be used for various purposes. One is action generation, but others are action understanding, space and action conscious awareness. At the basis of these multiple functions there is one functional mechanism: embodied simulation (Gallese 2005 a,b, 2006). By means of embodied simulation we do not just “see” an action, or an object located in space. Side by side with the sensory description of the observed stimuli, the motor schemata associated with these actions, or objects are evoked in the observer, “as if” he/she would be doing a similar action or interacting with that same object. Through the same mechanism conscious awareness of actions and spatial locations are generated. These functions are unlikely to be the only cognitive functions that the parieto-premotor circuits perform. Their capacity to “validate” experience renders them unique for acquiring knowledge—perhaps even abstract knowledge (see Lakoff and Johnson 1980, 1999; Gallese and Lakoff 2005)—about the external world. A challenge for future research will be to investigate the role played by parieto-premotor circuits in the most sophisticated cognitive endowments of our species, language and thought.

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