

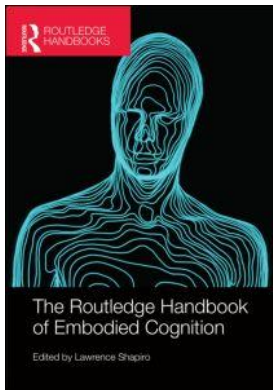
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5

THE ROLE OF THE MOTOR SYSTEM IN COGNITIVE FUNCTIONS

Laila Craighero

Cognitive embodiment refers to the hypothesis that cognitive processes of all kinds are rooted in perception and action. Recent findings in cognitive neuroscience revealed that the motor cortex, long confined to the mere role of action programming and execution, in fact, plays a crucial role in complex cognitive abilities.

The motor cortex, also defined as the agranular frontal cortex, is formed by a mosaic of at least seven anatomically and functionally distinct areas that appear to play different roles in motor control. Five of these areas receive their predominant cortical input from the parietal lobe, have a direct access to the spinal cord and have direct connections with the primary motor area.

The posterior parietal cortex was classically considered as a large association region into which information from different sensory modalities would converge to construct a single spatial map of the world. This map would be used for all purposes, e.g. walking, reaching objects, or describing a scene verbally. Lesion of this lobe and, in particular, of the inferior parietal lobule, produces a series of spatial deficits ranging from spatial distortions to spatial neglect. This view has been seriously challenged by a series of anatomical and functional data showing that the posterior parietal cortex is constituted by a multiplicity of architectonically and functionally defined areas, each of them involved in the analysis of different aspects of sensory information. Given the strong and specific connections of these parietal areas with the motor cortex, sensory information is then transformed into action (sensorimotor transformation). As a consequence, it is now widely accepted that there is not one single multi-purpose area for perception of space, rather the brain constructs multiple space representations that may be related to a specific class of actions (see Rizzolatti, Fadiga, Fogassi, and Gallese, 1997; Rizzolatti, Fogassi, and Gallese, 1997; Colby and Goldberg, 1999). Typically, each premotor area receives strong afferents from a single parietal area, and parietal and motor areas linked by predominant connections may share common functional properties. Thus, the parietal and premotor areas form a series of anatomical circuits largely independent of one another. In this chapter, parietofrontal circuits involving parietal visual areas, possibly involved in different aspects of visuomotor transformations for action, will be examined in more detail.

The first parietofrontal circuit we consider is constituted by the ventral premotor area F4 and the ventral intraparietal (VIP) area. Most neurons in this circuit discharge in association with

movements of the head or the arm (Gentilucci *et al.*, 1988). In particular, they discharge during the execution of specific actions, such as movements toward the mouth, or when the arm is moved toward a given spatial location. Furthermore, a large proportion of them respond to sensory stimuli. In particular, bimodal neurons respond both to visual three-dimensional stimuli and to tactile stimuli mostly applied to the face or arm (Gentilucci *et al.*, 1988; Graziano, Yap, and Gross, 1994; Fogassi *et al.*, 1996). Visual receptive fields (RFs) are formed by tridimensional portions of space located around the animal. They are generally limited in depth (from a few to about 40 centimeters) and almost always originate from the skin, thus forming an extension in space of the tactile RFs. Visual responses are very often selective for stimuli moving toward the tactile RFs and do not depend on the retinal position of the stimulus. Visual RFs remain anchored to the tactile ones regardless of gaze position, therefore, the VIP-F4 circuit seems to be involved in encoding peripersonal space according to a body-part-centered frame of reference and in transforming object locations into appropriate movements toward them. Furthermore, moving stimuli are not required to trigger F4 visual responses. In fact, Graziano, Hu, and Gross (1997) reported that F4 neurons continue to fire when, unknown to the monkey, the stimulus previously presented has been withdrawn, and the monkey “believes” that it is still near its body. Space representation in the premotor cortex can be generated, therefore, not only as a consequence of an external stimulation but also internally on the basis of previous experience. The interpretation of this result (Rizzolatti, Fadiga, *et al.*, 1997; Rizzolatti, Fogassi, *et al.*, 1997) is that the discharge of neurons reflects a potential action, a motor schema (Arbib, 1981; Jeannerod, Arbib, Rizzolatti, and Sakata, 1995), directed toward a particular spatial location (motor space). The presentation of a visual stimulus or the memory of its location (Graziano *et al.*, 1997) would automatically evoke one of these schemata, which, regardless of whether it is executed, maps the stimulus position in motor terms.

The second parietofrontal circuit involves the frontal eye field (FEF) region, in the prearcuate cortex, and the lateral intraparietal (LIP) area. The LIP-FEF circuit contains three main classes of neurons: neurons responding to visual stimuli (visual neurons), neurons firing in association with eye movements (movement neurons), and neurons with both visual- and movement-related activity (visuomovement neurons) (Andersen, Essick, and Siegel, 1985; Andersen, Bracewell, Barash, Gnadt, and Fogassi, 1990; Andersen and Gnadt, 1989; Barash, Bracewell, Fogassi, Gnadt, and Andersen, 1991; Bruce, 1988; Bruce and Goldberg, 1985; Goldberg and Segraves, 1989). Neurons responsive to visual stimuli respond vigorously to stationary light stimuli and their RFs are usually large. Movement-related neurons fire in relation to ocular saccades, most of them discharging before the saccade onset. Visuomovement neurons have both visual- and saccade-related activity. Visual RFs and “motor” fields are in register, that is, the visual RF corresponds to the end point of the effective saccade. Visual responses in both LIP and FEF neurons are coded in retinotopic coordinates (Andersen and Gnadt, 1989; Goldberg and Segraves, 1989). In other words, their RFs have a specific position on the retina in reference to the fovea. When the eyes move, the RF also moves. Most LIP neurons have, however, an important property. The intensity of their discharge is modulated by the position of the eye in the orbit (orbital effect). Now, if the position of the RF on the retina and the position of the eye in the orbit are both known, one can reconstruct the position of the stimulus in spatial (craniocentric) coordinates. This possibility may allow the LIP-FEF circuit to use eye position and retinotopic information for calculating an absolute position in space and for programming eye movements (Andersen and Mountcastle, 1983; Andersen *et al.*, 1985; Brotchie, Andersen, Snyder, and Goodman, 1995).

If one compares the properties of the LIP-FEF circuit with those of the VIP-F4 circuit, some analogies are immediately evident. Both circuits code space specifically for a particular motor

goal: eye movements in the case of the LIP-FEF circuit, body-part movements in the case of the VIP-F4 circuit. The differences possibly concern the different types of movements they control and the different sensory demands that eye movements and body-part movements pose. The way in which space is coded in the two circuits follows the same logic. A rather simple system based on retinotopic neurons, calculating also eye position, is sufficient for programming eye movements that are executed under the same load condition and, therefore, are stereotyped. The organization of body-part movements, which are characterized by a large variability in terms of load, speed and degree of freedom, requires multiple different frames of references. The difference between the properties of the LIP-FEF circuit, on one hand, and the VIP-F4 circuit, on the other, is probably a cue for understanding why there is no multi-purpose space map: the various motor effectors need different information and have different sensory requests and these cannot be provided by a unique map.

Therefore, this description of the neuronal representation of space coding seems to reflect a division of the space on the basis of the potential actions that can be performed in it. The space coded by the VIP-F4 circuit, and termed peripersonal space, is a space in which objects can be grasped and manipulated directly by the unaided use of the arm and the hand, and where the actions can lead to some consequence. Objects located beyond this space, the space coded by the LIP-FEF circuit and termed extrapersonal space, cannot normally be reached but only smelled, heard or seen. Yet, what happens when the unreachable space becomes reachable because of the use of a tool? Iriki, Tanaka, and Iwamura (1996) trained macaques to retrieve distant objects using a rake. In these monkeys, neuronal activity was recorded from the intraparietal cortex, where somatosensory and visual information is integrated. Neurons responding to both somatosensory and visual stimulation, namely “bimodal neurons,” were analyzed. Results showed that after the training, these neurons showed a visual receptive field including the entire length of the rake or covering the expanded accessible space. Therefore, it seems that the peripersonal space is not defined by metrical parameters (i.e. the length of our effectors) but by functional ones: if I am able “to do” something in a space then that becomes my peripersonal space. Inspired by these experiments, several researchers have investigated the behavioral effects of tool use in humans. These studies aimed to identify whether tool-assisted reaching for far stimuli would produce similar behavioral effects as direct reaching for nearby stimuli with the hands alone. Berti and Frassinetti (2000) examined the effect of tool use in a brain-damaged patient, whose neglect selectively affected the peripersonal space. When requested to show the midpoint of a drawn line, she put her mark further towards the right from the objective midpoint. However, when lines were presented in the extrapersonal space and she was requested to use a laser pointer, her performance was almost flawless. By contrast, when a long stick was used for the same far-line bisection, she showed a rightward bias again. One difference between a laser pointer and a long stick is their different capacity to be used in actions in the far space. The laser pointer simulates the eyes’ behavior: it is possible to focus it on a precise position of the far space but only to indicate it. In contrast, the stick simulates a finger behavior which is able to modify the state of the selected space region. For example, with some training, the use of a stick may allow the individual to turn on the light switch on the far wall, while the laser pointer does not permit this. The results of the Berti and Frassinetti (2000) experiment support the idea that when the stick made far space reachable, this became automatically coded by a neural network selective for peripersonal space where neglect was selectively present in the patient. Studies of crossmodal extinction in brain-damaged patients (Farnè and Làdavas, 2000; Maravita, Husain, Clarke, and Driver, 2001), of crossmodal congruency in normal participants (Maravita, Spence, Kennett, and Driver, 2002), of modulation of auditory peripersonal space during mouse use (Bassolino, Serino, Ubaldi, and Làdavas, 2010), and of

pseudo-neglect in real (Longo and Lourenco, 2006) and virtual environments (Gamberini, Seraglia, and Priftis, 2008) also support the view that tool use can modulate peripersonal space.

The last parietofrontal circuit involved in visuomotor transformations for action we consider is formed by the ventral premotor area F5 and the anterior intraparietal area. This is surely the most famous circuit among the three, possibly because the functional properties of its neurons are immediately interpreted as evidence of how cognitive processes may be rooted in perception and action. This circuit contains, among others, the so-called mirror neurons: a mirror neuron is a neuron that fires both when an animal acts and when the animal observes the same action performed by another (di Pellegrino, Fadiga, Fogassi, Gallese, and Rizzolatti, 1992; Gallese, Fadiga, Fogassi, and Rizzolatti, 1996). Thus, the neuron “mirrors” the behavior of the other, as though the observer were itself acting. Many researchers in cognitive neuroscience and cognitive psychology argue that mirror neurons may be important for understanding the actions of other people, and for learning new skills by imitation (Rizzolatti and Craighero, 2004). Some researchers also speculate that mirror systems may simulate observed actions, and thus contribute to theory of mind skills (Keysers and Gazzola, 2006) while others relate mirror neurons to speech abilities (Fadiga, Craighero, Buccino, and Rizzolatti, 2002; Théoret and Pascual-Leone, 2002) or to the human capacity to share emotions (Iacoboni, 2009).

In order to be triggered by visual stimuli, mirror neurons require an interaction between a biological effector (hand or mouth) and an object. The sight of an object alone, of an agent mimicking an action, of an agent performing an action with a tool (unless a long training is made, see Ferrari, Rozzi, and Fogassi, 2005) or of an individual making intransitive gestures are all ineffective. The type of object has no influence (grasping a piece of food or a geometric solid produces responses of the same intensity). Presenting widely different visual stimuli, all representing the same action, is equally effective (the same grasping mirror neuron responds to a human hand or to a monkey hand grasping an object). Similarly, the response is typically not affected if the action is done near or far from the monkey. It is also of little importance for neuron activation if the observed action is eventually rewarded (Gallese *et al.*, 1996). Some mirror neurons (strictly congruent) fire when the observed and executed motor acts are the same (for example, grasping with precision grip), whereas others (broadly congruent) fire when the observed motor act has the same goal as the executed motor act (for example, grasping), but can be achieved in a different way (for example, with both precision and whole-hand grips) (Rizzolatti, Fogassi, and Gallese, 2001). To activate mirror neurons, complete visual information is not necessary: some of them fire in response to actions, the final parts of which are hidden from view (Umiltà *et al.*, 2001). Furthermore, some mirror neurons respond not only to the sight of an action but also to the sound of an action (audiovisual mirror neurons, see Kohler *et al.*, 2002). In addition, so-called mouth mirror neurons have been reported, responsive to the observation of lip-smacking and communicative actions (Ferrari, Gallese, Rizzolatti, and Fogassi, 2003). By analyzing the characteristics of the stimuli evoking the activity of mirror neurons it appears that the only unifying parameter is the presence of the perceived action in the monkey’s motor repertoire. Indeed, a monkey in the forest would never simulate grasping an absent fruit, nor would it ever use pliers for peeling a banana. The monkey has no reason to execute those actions; they represent actions without any goal for the monkey. On the other side, the monkey may grasp either a fruit or a stone, it may decide to use a precision or a whole-hand grip to grasp something, it knows that if a mate is on a fruit tree and moves its hand behind a leaf then it is likely going to grab something, and it knows as well that when it breaks a peanut it will hear a contingent and specific noise. Furthermore, the monkey knows that when it has the intention to engage a mate in friendly interactions it has to lip-smack. Each of these actions has a purpose for the monkey: they all represent goal-related actions for the monkey.

Therefore, what is defining the activity of mirror neurons is not, as some claim, simply the presence of a transitive action, i.e. an action performed towards an object. A lip-smack is an intransitive action. However, lip-smacking is an action that the monkey typically performs to reach a specific goal and, consequently, it is part of its motor repertoire.

From these considerations it seems that the mirror neuron system works as a modality to encode goal-directed actions, just as the auditory system works to encode a sequence of waves of pressure that propagates through a compressible medium (i.e. a sound). Whenever a cue relative to an action is perceived the system is activated: whether it is the sight of someone who breaks a peanut, or the sound of someone breaking the peanut, or the sight of someone who puts a hand inside a bag where I know there are some peanuts. However, if the monkey knows that the peanut bag is empty, the mirror system is not activated (Umiltà *et al.*, 2001). For the monkey “to put a hand inside an empty bag” is not an action, because it serves no purpose. The mirror system does not encode movements which are not part of the individual’s motor repertoire, exactly as the auditory system does not encode electromagnetic radiation (i.e. a light). Possibly, movements which are not part of the individual’s motor repertoire are elaborated by the visual system as any other visual stimulus and are recognized and categorized exactly as would be stimuli such as a moving car or a tree that bends on a windy day (see also Shapiro, 2009).

There is convincing evidence that an action observation–action execution mirror system also exists in humans. This evidence comes from brain imaging, transcranial magnetic stimulation, electroencephalography, magnetoencephalography and psychophysical studies (see Rizzolatti and Craighero, 2004). However, the properties of the human mirror system differ dramatically from those of the monkey. In fact, this system may be active during the observation of both transitive and intransitive (non-object-directed) actions (Fadiga, Fogassi, Pavesi, and Rizzolatti, 1995; Brass, Bekkering, Wohlschläger, and Prinz, 2000; Buccino *et al.*, 2001) and during observation of pantomimes (Fadiga *et al.*, 2006). These differences, however, are canceled when we consider that humans commonly use intransitive actions and pantomimes to communicate or clarify concepts or feelings and sensations. This practice may have emerged from the capacity for abstraction, which allows humans to be free from the contingent relation with the objects (Fadiga *et al.*, 2006; Fadiga, Craighero, and D’Ausilio, 2009). Therefore, for humans both intransitive actions and pantomimes are goal-related actions and probably for this reason they are able to activate the human mirror system.

But for what reason do some primates possess a dedicated system to encode goal-directed actions? Why is it not sufficient to merely use the visual system? One possibility is to have the opportunity to reuse the accumulated knowledge regarding the consequences of our own actions and consequently to have the ability to anticipate and predict the outcome of others’ actions, enabling both collaborative or conflicting behaviors which form the basis of a social community (Rizzolatti *et al.*, 2001). There is much experimental evidence showing the possibility that the mirror system is involved in action prediction (Gangitano, Mottaghy, and Pascual-Leone, 2004; Montagna, Cerri, Borroni, and Baldissera, 2005; Craighero *et al.*, 2008); however, it is common knowledge that having the skill to perform an action makes one better at predicting and anticipating that action in others (Casile and Giese, 2006). This evidence is particularly clear in elite athletes as demonstrated by an experiment in which skilful basketball players, expert watchers (coaches and sports journalists) and novices were asked to judge the fate of free-throw shots at a basket (Aglioti, Cesari, Romani, and Urgesi, 2008). Participants were presented with movies showing free-throw basket shots performed by a professional basketball player. In half of the movies the ball landed in the basket and in the other half it did not. Video presentation was interrupted at 10 different durations (minimum 426 milliseconds; maximum 1,623 milliseconds). Participants were asked to choose among three possible

responses, namely, “Ball in,” “Ball out,” and “I don’t know.” Results showed that professional basketball players predict the outcome of free-throw shots earlier and more accurately than people who had no direct motor experience with a basketball. Furthermore, in the second part of the experiment the covert simulation of the observed action was tested by using transcranial magnetic stimulation technique and results showed that only athletes displayed a time-specific motor activation during observation of erroneous free throws. Indeed, the athletes showed motor activation that would appear to correct for the error in the shooter’s release. Unconscious awareness of such activation perhaps underlies the athletes’ superior ability to predict the success of the free throw.

Another possible function of a dedicated system for coding actions on the basis of accumulated motor knowledge is to have the opportunity to learn new motor abilities. Likely this function belongs exclusively to the human mirror system since it requires the possibility to interpret as goal-directed even strange movements performed by a dance teacher during a lesson. This opportunity would allow the activation of the human mirror system and the retrieval of the sensorimotor representation of a similar movement aiming at the same goal (e.g. “stand with hips turned out, heels touching together creating as close to a straight line with the feet as possible” may just be translated into: “stand with heels almost touching and feet turned outwards”). In this way, step by step, new motor abilities are acquired and new sensorimotor representations are generated permitting a more precise perception of the observed action. This hypothesis is supported by many different experimental results showing that mirror activation is greater for familiar actions but that even unfamiliar actions can cause it (Calvo-Merino, Glaser, Grezes, Passingham, and Haggard, 2005; Buccino *et al.*, 2004), that motor expertise modulates the activation of the human mirror system during the observation of dance moves, and that this activation is higher in individuals who had direct motor experience of the observed dance moves even when the experimenter controlled for the effect of visual familiarity with the moves (Calvo-Merino, Grezes, Glaser, Passingham, and Haggard, 2006). Moreover, learning complex dance patterns modulates neural motor activity during the observation of practiced as compared with visually familiar, but unpracticed, movements (Cross, Hamilton, and Grafton, 2006; Cross, Kraemer, Hamilton, Kelley, and Grafton, 2009).

The functional properties of the neurons present in parietofrontal circuits involved in visuo-motor transformations for action we reviewed in this chapter clearly indicate that the motor system plays a crucial role in complex cognitive abilities such as space coding, motor learning and prediction of others’ actions. Furthermore, we considered a series of experiments both in monkeys and in humans whose results are at odds with the traditional cognitivist view that percepts are built from elementary sensory information via a series of progressively more and more complex representations, suggesting the artificiality of a rigid wall between sensory and motor representations.

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