

# THE ROLE OF THE MIRROR NEURON SYSTEM IN MOTOR LEARNING

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Review

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## Abstract:

Following a classical perspective, acquiring a new motor skill implies moving from a declarative knowledge of the motor task to be learned to a procedural knowledge of it. Some recent research on the motor system challenges this view. In the ventral premotor cortex of a monkey, neurons have been discovered that discharge both when an animal executes a specific goal-directed action (i.e. grasping a piece of food) and when it observes the same or a similar action executed by a conspecific or an experimenter. These neurons are called "mirror neurons". In humans the mirror neuron system code for the execution and observation of goal-directed actions is executed with different biological effectors like the hand, the mouth, and the foot. The mirror neuron system has been demonstrated to be involved in action recognition, motor imagery and on line imitation of simple movements, which are already present in the motor repertoire of the acting individuals. Furthermore, in a very recent functional magnetic resonance image (fMRI) study, the involvement of this system in learning novel, complex hand actions has been tested. In the experiment musically naïve participants were asked to learn to play different guitar chords, after observing models given by an expert guitarist. The mirror neuron system has been found active in all phases of the motor learning process, namely from the observation of the model till the execution of it by the participants. These results strongly support the notion that learning a new motor pattern implies re-arranging the elementary motor acts constituting it in order to fit a given model. This is an operation that the brain apparently does within the motor system, without the involvement of any specific associative areas.

**Key words:** *action recognition, motor imagery, on-line imitation, complex hand action, motor cortex, premotor cortex, biological effector, audio-visual mirror neurons*

## DIE ROLLE VOM SPIEGELNEURONENSYSYSTEM IM MOTORISCHEN LERNEN

### Zusammenfassung:

Vom klassischen Standpunkt gesehen, das Erwerben einer neuen motorischen Fertigkeit impliziert das Überwechseln von deklarativem Kenntnis einer zu lernenden motorischen Aufgabe auf deren verfahrenstechnisches Kenntnis. Einige neueste Forschungen des motorischen Systems stellen diesen Standpunkt in Frage. Im ventralen prämotorischen Kortex einer Affe wurden die Neuronen entdeckt, die ausgeschüttelt werden, wenn das Tier eine spezifische auf das Ziel orientierte Aufgabe ausführt (z.B. Ergreifen eines Stückes des Nahrungsmittels) und wenn es entweder dieselbe oder ähnliche von einem anderen Affe oder einem Experimentator ausgeführte Bewegung realisiert. Diese Neuronen werden Spiegelneuronen genannt. Bei Menschen wird der Spiegelneuronensystem-Code für die Ausführung und Beobachtung von den auf ein Ziel orientierten Bewegungen, die mittels verschiedener biologischen Effektoren wie die Hand, der Mund oder der Fuß realisiert werden, realisiert. Das Spiegelneuronensystem zeigte sich in das Erkennen einer Bewegung, in der motorischen Vorstellung und in der parallelen Nachahmung von einfachen Bewegungen involviert zu sein, die schon im motorischen Repertoire von tätigen Individuen existiert. Außerdem in einer neuen Studie der funktionellen Magnet-Resonanz-Tomographie (fMRI) wurde die Rolle dieses Systems beim Erlernen neuer, komplexer Handbewegungen getestet. Im Experiment wurden die Teilnehmern, die sich in Musik nicht auskennen, gebeten, verschiedene Akkorde auf der Gitarre spielen zu lernen, nachdem sie die von einem Expert-Gitarristen durchgeführten Models beobachtet haben. Das Spiegelneuronensystem war aktiv in allen Phasen des motorischen Lernprozesses, d.h. angefangen von der Beobachtung eines Models bis zur dessen Ausführung. Diese Ergebnisse befürworten bedeutend die Ansicht, dass das Erlernen neuer motorischen Mustern eine Änderung von elementaren motorischen Bewegungen, die einen solchen Muster bilden, impliziert, um einem bestimmten Model zu entsprechen. Es handelt sich um eine Operation, die das Gehirn offensichtlich in dem motorischen System ausführt, ohne die Beteiligung von spezifischen assoziativen Bereichen.

**Schlüsselwörter:** *aktives Erkennen, motorische Vorstellung, parallele Nachahmung, komplexe Handbewegungen, motorischer Kortex, prämotorischer Kortex, biologischer Effektor, audiovisuelle Spiegelneuronen*

## Introduction

By motor learning we mean a series of processes linked to practice through which individuals can acquire new motor competence (Schmidt, 1991).

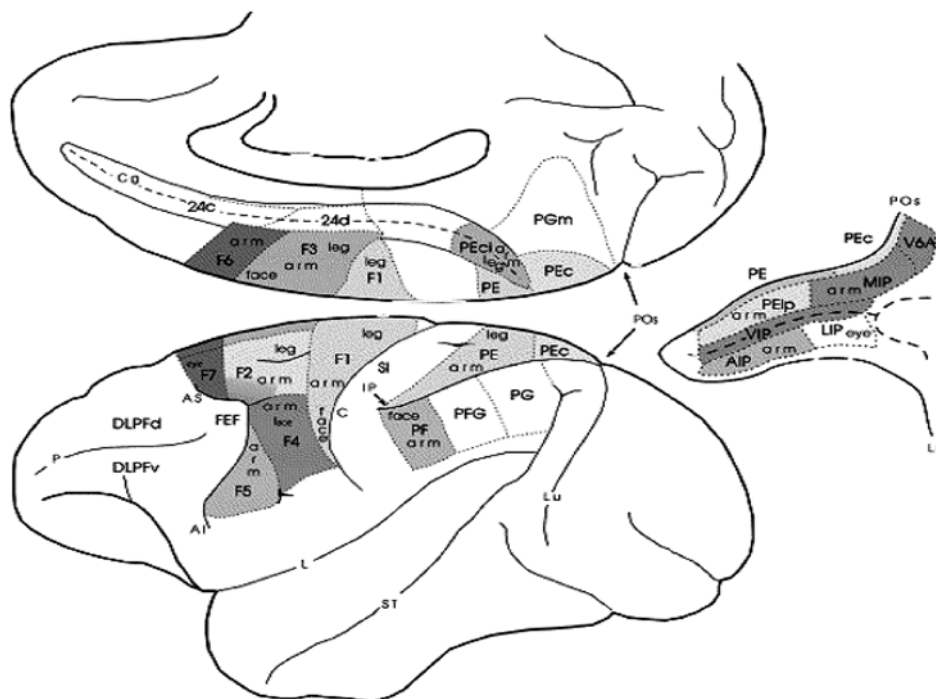
In order to learn a new motor skill, it is classically thought that individuals undergo three different phases: 1. *The cognitive phase*. During this phase, individuals try to learn the rules concerning a specific motor skill. For example, if an individual wants to learn to ride a bicycle he/she may try to define internally some rules: I must keep my body in this position... I must put my hands on the handlebars..., and so on. He/she therefore uses a declarative knowledge concerning the task he/she is going to learn. 2. *The associative phase*, during which an individual decomposes the motor task he/she is going to learn into more elementary motor components, distinguishing the relevant information for the task performance from the irrelevant. 3. *The automatic phase*. This is the phase during which individuals have developed practice and experience in doing the motor task so that they do it automatically. According to this view, during the acquisition of a new motor pattern individuals move from declarative knowledge of the motor task to procedural knowledge, when they can do the new motor task automatically.

Action observation and motor imagery play a fundamental role in motor learning. In this short review on motor learning presented here some recent experimental evidence on the organization of the motor system will be focused on. In particular, the features of a set of neurons, the so-called mirror neurons will be highlighted, showing that the motor representations used to execute an action overlap, to a certain extent, the motor representations responsible for other cognitive motor tasks such as the recognition and understanding of actions done by others, motor imagery and action imitation. Finally, some recent data will be reviewed showing that the mirror neuron system is indeed involved also when a new motor pattern has to be acquired.

## The mirror neuron system

### The mirror neuron system in a monkey

The notion of the motor system both in humans and in non-human primates has radically changed in recent times, and is now thought to include a large number of areas. The premotor cortex of a monkey's brain consists of various areas, defined on the basis of anatomical, histochemical, and physiological methods (Matelli, Luppino, & Rizzolatti, 1985). This modern parcellation of the motor system is presented in Figure 1.



**Figure 1. Parcellation of the motor system.** The figure shows that the organization of the motor system is more complex than previously thought. In fact, this system consists of numerous areas, each indicated in a monkey with the letter F (frontal) followed by a number. F1 corresponds to the classically defined primary motor cortex (area 4 of Brodmann); the premotor cortex (BA 6) is further divided into a ventral premotor cortex (LPMCv) and a dorsal premotor cortex (LPMCd). The ventral premotor cortex consists of two distinct areas: area F5 (BA 44 in humans), rostrally located, and area F4 (LPMCv in humans), caudally located. The dorsal premotor cortex is also composed of two areas: area F7, rostrally located (rostral LPMCd in humans) and area F2 (caudal LPMCd in humans), caudally located. On the medial surface of the hemisphere, the premotor cortex includes a caudal area (area F3, which corresponds to the classically defined SMA in humans) and a rostral area (area F6, also called pre-SMA in humans). (From Rizzolatti, Luppino, & Matelli, 1998)

One of these areas, area F5, is of particular interest because it contains a motor representation of mouth and hand object-directed actions (Rizzolatti et al., 1988). A set of these neurons that discharge during the execution of both hand and mouth object-directed actions also respond when a monkey observes another monkey or an experimenter performing the same or a similar action (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). These neurons are called mirror neurons because the observed action seems to be “reflected”, as in a mirror, in the motor representation for the same action of the observer.

The congruence between the motor action coded by the neuron and that triggering the same neuron visually may be very strict, in that only the observation of an action identical to that coded motorically by the neuron can activate it. More often, this congruence is broader, in that the observed and the executed action coded by the neuron match relatively to the goal of the action, rather than to the specific movements needed to perform it.

Certain important features of mirror neurons should be highlighted: During action observation, mirror neurons discharge only when a biological effector (a hand, for example) interacts with an object; if the action is performed with a tool, the neuron does not discharge. Furthermore, mirror neurons are not active when the observed action is simply mimicked, i.e. executed in the absence of the congruent object. Finally, mirror neurons do not discharge during the mere visual presentation of an object. Although mirror neurons were first described in the context of hand actions, a recent work has demonstrated that area F5 also contains mirror neurons that discharge during the execution and observation of mouth actions. Most of mouth mirror neurons become active during the execution and observation of mouth ingestive actions such as grasping, sucking or breaking food. Some of them, however, respond during the execution and observation of oral communicative actions such as lip-smacking (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003).

Since their discovery, it has been hypothesized that mirror neurons play an important role both in action recognition and in motor learning (Jeannerod, 1994). This hypothesis has been fully supported by a recent electrophysiological study (Umiltà et al., 2001) clearly showing that mirror neurons may infer the goal of an action. In the study, two experimental conditions were present: in the first one (vision condition) the animal could see the whole sequence of a hand object-directed action, in the second one (hidden condition) the final part of the action was hidden from the monkey's sight by means of a screen. However, the animal was shown that an object, for example a piece of food,

had been placed behind the screen, which prevented the observation of the final part of the executed action. The results of the study showed that mirror neurons discharge not only during the observation of a hand object-directed action, but also when the final part of it is hidden.

A recent experiment has demonstrated that, besides visual properties, about 15% of mirror neurons also respond to the presentation of the typical sound of an action. These neurons are called audio-visual mirror neurons (Koehler et al., 2002). These neurons could be used to understand actions performed by other individuals even if only heard. It has been argued that these neurons code the action content, which may be triggered either visually or acoustically, thus representing a possible step for the acquisition of language.

### **The mirror neuron system in humans**

There is increasing evidence that a mirror neuron system also exists in humans. Data supporting this notion come from experiments carried out with neurophysiological, behavioral, and brain imaging techniques.

#### *Neurophysiological studies*

The first evidence, albeit only indirect, of the existence of a mirror neuron system in humans was provided by Fadiga and associates (1995) who delivered single pulse transcranial magnetic stimulation (TMS) to normal volunteers while observing an experimenter doing different object-directed hand actions. As control conditions, single pulse TMS was delivered during the observation of the same objects, observation of an experimenter tracing geometrical figures in the air with his arm, and dimming light detection. Motor evoked potentials (MEPs) were recorded from extrinsic and intrinsic hand muscles. Results showed that the hand action observation, but not the other conditions, led to an increase of MEPs in those same hand muscles involved in the actual execution of the observed action by the observer. These results have been recently confirmed by Strafella and Paus (2000). Using TMS, Gangitano and associates (2001) found that during the observation of hand actions there is not only an increase of MEP amplitude in the muscles involved in the actual execution of the observed action, but that the MEPs are modulated in a fashion strictly resembling the time-course of the observed action. Taken together, these TMS data support the notion of a mirror neuron system, matching action execution and action observation.

The involvement of the mirror neuron system during action observation was also demonstrated by Hari and associates (1998), using magnetoencephalography (MEG). With this technique a suppression

of the 15-25 Hz activity during both the execution and the observation of object-directed hand actions was found. Similar results were obtained in a study using quantified electroencephalography, showing a block of "mu" activity in the same conditions (Cochin, Barthelemy, Roux, & Martineau, 1999). More recently, by means of chronically implanted subdural electrodes, a decrease of alpha band absolute power over the primary motor cortex and the Broca's region during the execution and observation of finger movements was shown (Tremblay et al., 2004).

All of these studies not only provide evidence that observation and execution of action share common neural substrates in the humans, but also demonstrate that action observation produces an increase in the excitability of the corticospinal pathway.

### *Behavioral studies*

Neuropsychological studies also provided evidence in favor of the existence of a mirror neuron system in humans. Brass and associates (2000), for example, investigated how the observation of a specific movement can influence the execution of that movement by means of a stimulus-response compatibility paradigm. Using a reaction time paradigm, the authors contrasted the role of the observation of symbolic cues as compared to the observation of finger movements in the execution of finger movements. Subjects were faster in responding when they were prompted by the observation of movement. Moreover, the degree of similarity between the observed and executed movement led to a further advantage in the execution of the observed movement. These results provide strong evidence for the influence of the observed movement on the execution of that movement.

Craighero and associates (2002) found similar results in a study in which normal volunteers were asked to prepare to grasp as fast as possible a bar oriented either clockwise or counterclockwise, after presentation of a picture showing the right hand. Two experiments were carried out. In the first experiment the picture represented a mirror image of the final position of the hand required to grasp the bar. The second experiment included the same stimuli as in the first one, plus two additional pictures, 90° rotations of the hand in both leftward and rightward directions. In both experiments, responses of the participants were faster when the hand orientation of the picture corresponded to that achieved by the hand at the end of the action, when actually executed. Moreover, the responses were globally faster when the stimuli were not rotated.

Summing up, these behavioral studies not only reinforce the notion of a mirror neuron system in humans, but also suggest facilitation of execution when preceded by motor observation.

### *Brain imaging studies*

The neurophysiological and behavioral studies do not provide insight into the localization of the mirror neuron system in humans. This issue has been addressed by a number of brain imaging studies.

In an early positron emission tomography (PET) experiment, aimed at identifying the brain areas active during action observation, Rizzolatti and associates (1996b) compared hand action observation with observation of an object, and found activation in the Broca's area of the left inferior frontal gyrus, the middle temporal gyrus, and the superior temporal sulcus. Although the Broca's area is classically considered an area devoted to speech production, it has recently been demonstrated that this area also contains a motor representation of hand actions (Binkofski et al., 1999; Binkofski & Buccino, 2004). Given the homology between the Broca's area and area F5 in a monkey (Petrides & Pandya, 1997; Rizzolatti & Arbib, 1998; Binkofski & Buccino, 2004), where mirror neurons were originally discovered, this study provided the first evidence of the anatomical localization of the mirror neuron system for hand actions in humans.

A recent fMRI study showed that the mirror neuron system in humans is complex and related to body actions performed not only with the hand, but also with the foot and the mouth. Buccino and associates (2001) asked normal participants to observe video-sequences showing different actions performed with the mouth, the hand, and the foot. The observed actions could be either object-directed (the mouth/hand/foot acted on an appropriate object, physically present in the scene) or mimicked (the mouth/hand/foot action was performed in the absence of the congruent object). The following actions were presented: biting an apple, grasping a cup, grasping a ball, kicking a ball, and pushing a brake pedal. As a control, the participants were asked to observe a static image of each action.

The observation of both object directed and mimicked actions, compared to the observation of a static image of the same action, led to the activation of different sectors in the premotor cortex and the Broca's region, depending on the effector involved in the observed action. The different sectors largely overlapped those where classical studies (Penfield, & Rasmussen 1950) had shown a somatotopically organized motor representation of the different effectors involved in the execution of the observed actions. Moreover, during the observation of object-directed actions, distinct sectors in the inferior parietal lobule were also active, including areas inside and around the intraparietal sulcus, again depending on the effector involved in the observed action. The results of this study are presented in Figure 2.

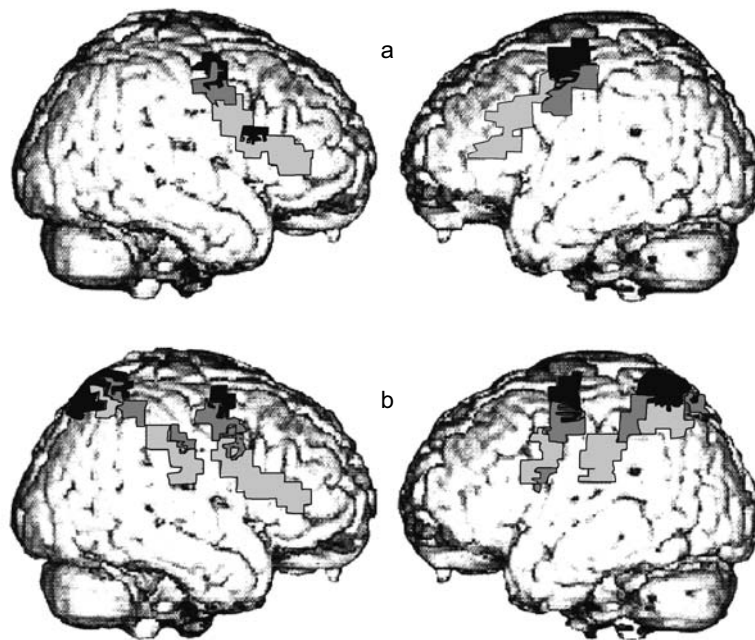


Figure 2. **Mirror neuron system in humans.** Somatotopic fMRI activations in parietal and premotor regions during the observation of intransitive (a) and transitive (b) actions in humans.  = mouth related movements;  = hand related movements;  = foot related movements. (From Buccino et al., 2001)

On the whole, this study strongly supports the claim that, as in the actual execution of actions, action observation recruits different, somatotopically organized fronto-parietal circuits (Jeannerod et al., 1995; Rizzolatti, Luppino, & Matelli 1998). In this context, it is worth noting that mirror neurons, similar to those described in area F5, have recently been reported in the inferior parietal lobule of a monkey (area PF) (Gallese, Fogassi, Fadiga, & Rizzolatti, 2002).

### The mirror neuron system and motor imagery

In a broad sense, motor imagery refers to the capacity to “mentally rehearse simple or complex motor acts that are not accompanied by overt body movements” (Jeannerod, 1994). It represents the voluntary effort of an individual to imagine himself/herself executing a specific action. As underlined above, motor imagery may help to learn a new motor pattern. In fact there is evidence that motor imagery, similarly to motor execution, may improve performance in different categories of people, including athletes and musicians.

Although the definition of motor imagery appears simple, when individuals are required to do motor imagery, they apply different strategies. They may (a) produce a visual representation of the moving limb, in which case he/she is a (third-person) spectator of the movement (this is more properly defined as visual imagery), or (b) mentally simulate the movement, with a kinesthetic feeling of the

movement. In this case the person is a (first-person) performer of the movement (this is sometimes referred to as kinetic imagery and fits the general definition of motor imagery reported above).

Since kinetic imagery shares more physiological features with the execution of movement than visual imagery does, it has been associated more closely with motor functions per se such as motor preparation, imitation, and anticipation, and the refining of motor abilities (Decety et al., 1994; Porro et al., 1996; Fadiga et al., 1999; Rossini, Rossi, Pasqualetti, & Tecchio, 1999; Stephan, 1996; Jeannerod, 2001; Gerardin et al., 2000; Hanakawa et al., 2003).

As a whole, brain imaging studies using PET or fMRI, have hardly differentiated between visual imagery and kinetic imagery. In general, studies have shown that several areas, including those belonging to the mirror neuron system, are activated during motor imagery tasks. Included in these active regions are the following: supplementary motor area, superior and inferior parietal lobules, dorsal and ventral premotor cortices, pre-frontal areas, inferior frontal gyrus, superior temporal gyrus, primary motor cortex (M1), primary sensory cortex, secondary sensory area, insular cortex, anterior cingulate cortex, superior temporal gyrus, basal ganglia and cerebellum. This extensive activation suggests a complex distributed circuit for motor imagery that shares several cortical regions fundamentally involved in action execution and action observation.

## The mirror neuron system in imitation

### On-line imitation of simple movements

Motor imitation is often regarded as an elementary cognitive task. Recent research, coming from different fields, demonstrates that this assumption is not true. There is clear evidence that imitation is a faculty developed specifically in humans and intrinsically linked to language and culture (Rizzolatti, Fadiga, Fogassi, & Gallese, 2002). Action imitation inherently implies motor observation, motor imagery, and actual execution of the movements.

Involvement of the mirror neuron system in imitation was recently demonstrated by a series of brain imaging studies. Using fMRI, Iacoboni and associates (1999) scanned normal human volunteers while they were lifting a finger in response to (a) visual presentation of the target action on a screen ("imitation"); (b) to a symbolic cue; or (c) to a spatial cue. The results showed that the *pars opercularis* of the left inferior frontal gyrus (IFG), grossly corresponding to the Broca's region, the right anterior parietal region, the right parietal operculum, and the right STS region were more active during imitation than during the other motor conditions. Experiments by Koski and associates (2002) and by Grèzes, Armony, Rowe, & Passingham (2003) confirmed the importance of the Broca's area in imitation tasks, particularly when the action to be imitated was object-directed. Nishitani and Hari (2000; 2002) performed two MEG studies in which they investigated imitation of grasping actions and facial movements. The first study confirmed the importance of the left IFG (largely corresponding to the Broca's region) in imitation. In the second study (Nishitani & Hari, 2002), volunteers observed still pictures of verbal and non-verbal (grimaces) lip forms, and either imitated them immediately after seeing them, or made similar lip forms spontaneously. During lip form observation, cortical activation moved from the occipital cortex to the superior temporal region, the inferior parietal lobule, IFG, and finally to the primary motor cortex. The activation sequence during imitation of both verbal and non-verbal lip forms was the same as during observation.

Taken together, these data strongly support the notion that the basic neural circuit subserving imitation largely overlaps that active during action observation. They also indicate that a direct mapping of the observed action and its motor representation takes place in the posterior part of IFG.

The importance of the "pars opercularis" of IFG in imitation was further demonstrated using repetitive TMS by Heiser and associates (2003). The task used in the study was essentially the same used by Iacoboni and associates (1999). The results showed that following stimulation of both the Broca's area and its right homologue, there was significant im-

pairment in the imitation of finger movements. The effect was absent when the finger movements were performed in response to spatial cues.

In the experiments reviewed above the individuals were asked to imitate "on-line" highly practiced, simple movements made by another individual. The movements to be imitated were already part of the observer's motor repertoire. Such "on-line" imitation was also studied by Tanaka and Inui (2002), who, however, asked the participants to imitate relatively complex hand or arm postures. This study also found only that a finger condition showed significant activation in the Broca's area, whereas a hand condition did not.

### Imitation learning

In the experiments mentioned thus far, imitation has consisted of matching observed movements or actions to pre-existing motor schemata, i.e. to motor actions which were already part of the observer's motor repertoire. By contrast, a recent study investigated motor learning of a novel motor pattern by action observation (Buccino et al., 2004). The basic task during event-related fMRI was the imitation by naive participants of guitar chords played by an expert guitarist. The four events of which the imitation condition typically consisted of, were performed in order – observation of guitar chords, pause, execution of the observed chords, and baseline. The three control conditions were observation of the chords (with no subsequent motor activity), observation of the chords followed by execution of the unrelated motor actions (e.g., grasp-release of the guitar neck), and free execution of the guitar chords.

The results showed that the observation event was associated with activation of a cortical network formed by the inferior parietal lobule and the ventral premotor cortex (Pmv) plus the *pars opercularis* of IFG (mirror neuron system). This circuit was also active during observation in the two control conditions. The strength of activation related to action observation was much stronger during imitation than during the control conditions, and was associated with additional activation in anterior mesial areas, superior parietal lobule, and in the prefrontal cortex.

The pause event during action imitation was aimed at uncovering the activation related to novel motor pattern formation and consolidation. Activation during this event involved the same basic circuit as in action observation, but with some important differences, including an increase of superior parietal lobule activation, activation of dorsal premotor cortex (Pmd), and most interestingly, a dramatic increase in the extension and strength of the prefrontal cortex activation (possibly BA 46) and of areas of the anterior mesial wall. Finally, during the execution event, activation involved the senso-

rimotor cortex contralateral to the hand executing the observed chords.

These data show that the neural substrates responsible for the building up of new motor patterns largely coincide with the key centers of the mirror neuron system. Although these fMRI experiments do not provide information on the mechanism underlying imitation, it is plausible that during the learning of new motor patterns by imitation, the observed actions are decomposed into elementary motor acts that activate, by a mirror mechanism, the corresponding motor representations in the inferior parietal lobule, in the ventral premotor cortex and in the *pars opercularis* of IFG. Once these motor representations are activated, they are recombined, to fit the observed model. This recombination appears to occur inside the mirror neuron system, with area 46 possibly playing a fundamental orchestrating role.

## Conclusion

The experimental data reviewed so far clearly show that the motor system is not only involved in the execution of actions but also in other cognitive motor functions. Both when an action is actually done and when it is only covertly rehearsed (as in

the S states defined by Jeannerod, 2001) the same neural structures are involved. In particular, the mirror neuron system is endowed with a mechanism allowing individuals to understand actions done by others just by matching the observed actions with their correspondent motor representations in the observer's brain. Moreover the ventral premotor cortex and the inferior parietal lobule, the cortical regions belonging to the mirror neuron system are also involved in the motor imagery of actions and in the "on-line" imitation of others' actions. Even more important to the aim of the present review, is the fact that even when a new motor skill has to be learned, the mirror neuron system is active from the observation of the model till the execution of an action fitting the model. This capacity of the mirror neuron system may rule out the necessity for the brain to have areas specifically devoted to higher order motor functions. Learning a new motor pattern, therefore, could mean recombining in a new order the basic motor acts constituting it. Following the paper of Buccino and associates (2004), this recombination seems to occur within the mirror neuron system and not in the associative areas, as assumed by theories proposing that motor learning moves from a declarative knowledge of the actions to be learned to a procedural knowledge of them.

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## ULOGA SUSTAVA ZRCALNIH NEURONA U MOTORIČKOM UČENJU

### Sažetak

#### Uvod

Pod pojmom "motoričko učenje" razumije se niz procesa povezanih s vježbanjem tijekom kojih osoba usvaja nova motorička znanja i razvija motoričke sposobnosti (Schmidt 1991). Tradicionalno je tumačenje da osoba tijekom usvajanja nove motoričke vještine prolazi tri različite faze: 1. kognitivnu fazu (učenje pravila specifične motoričke vještine); 2. asocijativnu fazu (rašćlanjivanje motoričkog zadatka na elementarne motoričke komponente, razlučivanje relevantnih i irelevantnih informacija za izvođenje zadatka) i 3. automatsku fazu (uvježbanost i iskustvo u izvođenju motoričkog zadatka, tako da se zadatak izvodi automatski). Prema tom stajalištu, tijekom usvajanja novog motoričkog obrasca, osoba prelazi s deklarativnog znanja o motoričkom zadatku na proceduralno znanje o izvedbi. Novija istraživanja o motoričkom sustavu, međutim, osporavaju ovo gledište.

#### Sustav zrcalnih neurona

##### Sustav zrcalnih neurona kod majmuna

Spoznaje o motoričkom sustavu kod čovjeka, kao i kod čovjekolikih majmuna, u novije su se vrijeme radikalno promijenile te se danas smatra da uključuje velik broj područja mozga. Jedno od njih, područje F5 ventralne premotoričke kore mozga čovjekolikih majmuna, sadrži motoričku reprezentaciju prema cilju usmjerenih radnji ustiju i šaka (Rizzolatti et al., 1988). U tom je području otkrivena skupina neurona kod kojih je prisutno izbijanje i kad sama životinja izvodi specifičnu, cilju usmjerenu radnju (npr. posezanje za komadom hrane), ali i u slučaju kad ona samo promatra jednaku ili sličnu radnju u izvođenju druge životinje ili pak istraživača (Gallese et al., 1996; Rizzolatti et al., 1996a). Ti se neuroni nazivaju zrcalnim neuronima jer se doima kao da se promatrana radnja "reflektira" u promatračevoj motoričkoj reprezentaciji iste radnje, kao u zrcalu.

Od samog otkrića, pretpostavljalo se da zrcalni neuroni igraju važnu ulogu, kako u prepoznavanju radnje, tako i u motoričkom učenju (Jeannerod, 1994). Te je pretpostavke u potpunosti poduprlo recentno elektrofiziološko istraživanje (Umiltà et al., 2001). Jedan od novijih eksperimenata pokazao je da oko 15% zrcalnih neurona, osim na vizualna svojstva, reagira i na prezentaciju specifičnog zvuka određene radnje. Ti se neuroni nazivaju audio-vizualnim zrcalnim neuronima (Kohler et al., 2002).

##### Sustav zrcalnih neurona kod čovjeka

Sve je više dokaza o postojanju sustava zrcalnih neurona i kod čovjeka. Podaci na kojima se temelje ova saznanja proizlaze iz istraživanja provedenih korištenjem neurofizioloških i bihevioralnih

tehnika i metoda prikazivanja mozga (engl. *brain imaging*).

##### Neurofiziološka istraživanja

Prvi, iako samo indirektni, dokaz o postojanju sustava zrcalnih neurona kod čovjeka pružilo je istraživanje u kojem je primijenjena transkranijalna magnetska stimulacija (TMS) kod zdravih dobrovoljaca koji su promatrali istraživača u izvođenju različitih, cilju usmjerenih, kretnji šake (Fadiga et al., 1995). Ti su rezultati nedavno potvrđeni (Strafella and Paus, 2000; Gangitano et al., 2001). Daljnja istraživanja na tom području koristila su se magnetoencefalografijom (MEG) (Hari et al., 1998), kvantificiranom elektroencefalografijom (Cochin et al., 1999) i trajno implantiranim subduralnim elektrodama (Tremblay et al., 2004).

##### Bihevioralna istraživanja

Brass i suradnici (2000) su, korištenjem paradigme kompatibilnosti podražaj-odgovor, ispitivali kako promatranje specifičnog pokreta može utjecati na samo izvođenje tog pokreta. Dobiveni rezultati pružili su čvrst dokaz o utjecaju promatranja pokreta na izvođenje istog pokreta. Slične rezultate dobili su Craighero i suradnici (2002).

##### Istraživanja metodama prikaza mozga (*brain imaging*)

U ranom istraživanju, usmjerenom na utvrđivanje područja mozga aktivnih tijekom promatranja radnji, u kojemu je korištena pozitronska emisijska tomografija (PET), Rizzolatti i suradnici (1996b) su otkrili aktivaciju u Brokinom području lijeve donje čeonje vijuge, srednje sljepoočne vijuge i gornjeg sljepoočnog žlijeba. Ovo je istraživanje pružilo prvi dokaz o anatomskoj lokalizaciji sustava zrcalnih neurona za kretanje šake kod čovjeka.

Nalazi vrlo recentnog istraživanja funkcionalnom magnetskom rezonancijom (fMRI) (Buccino et al., 2001) snažno podupiru tvrdnju da se, kao kod stvarnog izvođenja kretanja, i kod promatranja kretanja regrutiraju različiti, somatotopski organizirani čeonno-tjemeni krugovi (Jeannerod et al., 1995; Rizzolatti et al., 1998b).

##### Sustav zrcalnih neurona i motorička predodžba

Motorička predodžba predstavlja voljno nastojanje osobe da zamisli sebe u izvođenju određene radnje. Motorička predodžba može pomoći u učenju novog motoričkog obrasca. Kada se od pojedinaca zatraži da stvore motoričku predodžbu, oni mogu primijeniti različite strategije. Oni mogu: (a) stvoriti vizualnu reprezentaciju ekstremiteta u pokretu (vizualna predodžba) ili (b) mentalno simulirati pokret, uz kinestetički osjećaj pokreta (kinetička predodžba).

S obzirom na to da kinetička predodžba dijeli više fizioloških obilježja s izvođenjem pokreta od vizualne predodžbe, više je povezivana sa samim motoričkim funkcijama (Decety et al., 1994; Stephan, 1996; Porro et al, 1996; Fadiga, 1999; Rossini et al, 1999; Jeannerod, 2001; Gerardin, 2000; Hanakawa et al., 2003).

Ukupno gledano, istraživanja u kojima su za prikazivanje mozga korištene PET ili fMRI, jedva da su pokazala razlike između vizualnih i kinetičkih predodžbi. Općenito, istraživanja su pokazala da se tijekom zadataka motoričkog predočavanja opsežno aktiviraju različita područja, uključujući ona koja pripadaju sustavu zrcalnih neurona. To sugerira postojanje složenog distribuiranog neuralnog kruga motoričke predodžbe koji uključuje i različita kortikalna područja u osnovi uključena u izvođenje i opažanje radnje.

## **Uloga sustava zrcalnih neurona u imitaciji**

### **Paralelna (on line) imitacija jednostavnih pokreta**

Motorička imitacija se često smatra elementarnim kognitivnim zadatkom. Novija istraživanja pokazuju da ta tvrdnja nije točna. Postoje jasni dokazi o tome da je imitacija sposobnost koja je specifično razvijena kod čovjeka te je intrinzično povezana s jezikom i kulturom (Rizzolatti et al., 2002). Imitacija radnje inherentno uključuje motoričko opažanje (opservaciju), motoričku predodžbu i samo izvođenje pokreta.

Uključenost sustava zrcalnih neurona u imitaciji nedavno je dokazana nizom istraživanja metodama prikaza mozga (Iacoboni et al., 1999; Koski et al., 2002; Grèzes et al., 2003; Nishitani and Hari, 2000, 2002; Heiser et al., 2003; Tanaka et al., 2002). U tim se istraživanjima od ispitanika tražilo da izravno, on line imitiraju visoko uvježbane, jednostavne pokrete koje je izvodila druga osoba. Pokreti koje je trebalo imitirati spadali su u već postojeći motorički repertoar opažača/ispitanika. Ukupno gledano, rezultati spomenutih studija snažno podupiru tvrdnju da se

osnovni neuralni krug koji omogućuje imitaciju u velikoj mjeri preklapa s neuralnim krugom aktivnim tijekom opažanja radnje. Rezultati također ukazuju na to da se izravno stvaranje mape promatrane kretnje/radnje te njena motorička reprezentacija zbivaju u stražnjem dijelu donje čeonje vijuge.

### **Učenje imitacijom**

U recentnom istraživanju proučavalo se motoričko učenje novog motoričkog obrasca promatranjem kretnje (Buccino et al., 2004). Od glazbeno neobrazovanih ispitanika zatraženo je da nauče odsvirati različite gitarističke akorde na temelju promatranja i oponašanja profesionalnog gitarista koji je svirao akorde. Uočeno je da je sustav zrcalnih neurona bio aktivan u svim fazama procesa motoričkog učenja, tj. od opažanja primjera do samog izvođenja primjera od strane ispitanika. Ti rezultati snažno podupiru teoriju prema kojoj učenje novog motoričkog obrasca podrazumijeva preraspodjelu osnovnih motoričkih kretnji koje ga tvore radi uklapanja u zadani model. Čini se da je to operacija koju mozak izvodi u potpunosti unutar motoričkog sustava, bez uključivanja specifičnih asocijativnih područja.

### **Zaključak**

Spomenuti rezultati istraživanja jasno pokazuju da motorički sustav nije uključen samo u izvođenje aktivnosti, nego i u druge kognitivne motoričke funkcije. Štoviše, ventralna premotorička kora i donji tjemeni režanj, kortikalna područja koja pripadaju sustavu zrcalnih neurona, također su uključeni u motoričku predodžbu radnji, kao i u imitaciju tuđih kretnji. Čak i prilikom učenja nove motoričke vještine, sustav zrcalnih neurona je aktivan od promatranja obrasca do izvođenja radnje koja odgovara obrascu. Učenje novog motoričkog obrasca bi, stoga, moglo predstavljati kombiniranje osnovnih motoričkih kretnji koje ga sačinjavaju na nov način. Izgleda da se ta rekombinacija zbiva unutar sustava zrcalnih neurona, bez uključivanja specifičnih asocijativnih područja.