9 Is the Motor Cortex Only an Executive Area? Its Role in Motor Cognition

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9.1 INTRODUCTION

The classical view of the primary motor cortex (M1) holds that it is an area devoted to transferring to motor execution messages that have been elaborated upstream in the cerebral cortex. Anatomically, M1 is the site of the convergence of inputs from the premotor cortex and basal ganglia; it is also the main site of the origin of the pyramidal tract and of direct cortico-motoneuronal connections. Early functional studies using direct cortical stimulation had concluded that the role of the motor cortex is limited to selecting the proper muscular addresses and encoding muscular force for executing a movement. To quote Penfield’s Ferrier Lecture,1 “Movement produced by stimulation of the motor cortex takes place most often in those members of the body which are capable of dextrous and complicated voluntary activity, and yet the movements thus produced are never dextrous nor purposeful.” And, in addition, “The conscious patient is never deceived into believing that he made the movement himself. He knows he did not plan it” (p. 344). This finding, which is
confirmed by the everyday practice of transcranial magnetic stimulation (TMS),
contrasts with the effects of stimulation of other more rostral motor areas. Stimulation
of lateral area 6 by Penfield and Boldrey,2 although it elicited no overt move-
ments, frequently elicited an intense “desire to move.”

More recently, however, experimental data have pointed to the fact that the
relation of motor cortex activity to the production of movements is not as simple as
it was thought to be on the basis of early stimulation experiments. This revision of
motor cortical function originated from two main lines of research, dealing first with
the plasticity of the somatotopic organization of M1, and second with its involvement
in cognitive functions.

9.2 RECENT FINDINGS REGARDING THE PRIMARY
MOTOR CORTEX

The somatotopic organization of M1 is unstable. It can be radically altered in a
number of situations, such as peripheral changes in neuromuscular connections or
motor learning and training. It has been known for more than 10 years that motor
cortical somatotopy in animals is subject to a vast amount of reorganization following
amputation of a limb or peripheral nerve lesion.3 In man, as in rats, the cortical
territory controlling the amputated joints tends to shrink, whereas the territory
controlling remnant adjacent joints tends to expand.4 For example, following ampu-
tation of a hand, the territory of the fingers will be invaded by more proximal joints
of the same limb (e.g., elbow and shoulder), or even by the face. It was suspected,
but not proven until recently, that this plastic phenomenon is reversible. One case
of hetero-transplantation of the two hands several years after bilateral amputation
at the level of the mid-forearms was studied by Giraux et al.,5 using fMRI for
mapping the activation of the motor cortex. Before surgery, the areas corresponding
to the two hands were mapped by asking the subject to “extend” or “flex” his
(missing) fingers. Execution of these movements was controlled by palpating finger
extensors and flexors at the level of the stump. Six months after surgery, the hand
areas were mapped during movements of the grafted hands. The comparison of
activation before and after surgery revealed that the hand areas on either side, which
were initially reduced to the most lateral part of the normal hand area close to the
face area, reexpanded medially to reoccupy its full territory. Similarly, the elbow
area, which had invaded a large section of the hand area, was pushed back medially
to its normal anatomical location.

Motor cortical reorganization following amputation is associated with subjective
sensory phenomena, like phantom pain.6,7 Partial restoration of the normal topogra-
phy by training reduces phantom pain. Lotze et al.8 showed that the extensive use
of a myoelectric prosthetic device by the amputee, because it prevents cortical
reorganization, has a positive effect on phantom pain. Giraux and Sirigu9 also showed
that reexpansion of the hand area by training resulted in a decrease in phantom pain.
The visuomotor training method used by Giraux and Sirigu consisted in transferring,
by way of mirrors, the image of the normally moving limb at the location of the
paralyzed limb. After a few sessions, the patient imagined his paralyzed limb moving,
and this resulted in reexpanding the atrophied corresponding primary motor cortex. The influence of imagined movements on M1 activity will be discussed again in another section.

Plastic modification of M1 somatotopy is not limited to peripheral changes such as amputation. It is also observed during motor training. Neuroimaging studies show that long-term training of finger movements produces not only an increase in the amplitude of the activation of the trained pixels, but also an enlargement of the finger cortical area.\textsuperscript{10,11} Although this effect of training can be partly explained by peripheral factors (e.g., the increase in reafferent input from the moving limb during repetitive movements; see Reference 12), it is also clearly influenced by central factors. Indeed, as will be reviewed below, the same effect of training can be observed in the absence of overt movements from the trained limb. Thus, M1 is liable to long-term changes in its intrinsic arrangement and connectivity, an experimental fact that would not be expected from a system devoted to transmitting executive commands, and that opens new possibilities for reinterpreting the role of M1 in motor functions.

The second set of data that leads to a reconsideration of motor cortex function arises from experiments showing the role of the motor cortex in cognitive activities that are related to motor function, but where no movement occurs. Georgopoulos and his colleagues first demonstrated in the monkey the existence of orderly changes in activity of M1 neurons during a cognitive operation. In this experiment, a monkey was instructed to perform an arm movement directed to a virtual target different from the one shown to her. During this process of target selection preceding execution of the movement, the activity of the neuronal population coding for the direction of the movement (the population vector) progressively changed from the direction of the target shown to the monkey to the direction of the virtual target, suggesting that the animal was performing a mental rotation of the population vector until it matched the instructed direction.\textsuperscript{13}

According to Georgopoulos,\textsuperscript{14} the primary motor cortex could be considered a cognitive area — i.e., an area involved in cognitive motor processes — rather than simply as an area devoted to motor execution and control of the spinal level. The core of this chapter will be devoted to examining the role of the motor cortex in cognitive operations that remain covert — i.e., where the action itself is not executed. In this category are included a variety of mental states related to action which fit the broad concept of motor representations, such as motor imagery or action observation. The key question will be this: if M1 is an executive area and if no overt movement occurs in these situations, why should M1 be involved? The tentative answer that will be given to this question is that M1 activation during cognitive motor operations is part of a neural process of simulation that serves as the basis of action representations.

### 9.3 THE FUNCTIONAL ANATOMY OF MOTOR REPRESENTATIONS

Neuroimaging techniques have greatly contributed to the functional anatomy of those purely mental states devoted to the representation of action. Following the pioneer
papers showing changes in regional cerebral blood flow during mental imagery,\textsuperscript{15,16} the pattern of cortical activity during both motor imagery and action observation has been extensively investigated.

Many studies using functional brain imaging by magnetic resonance (fMRI) reported activation of the sensorimotor cortex during motor imagery.\textsuperscript{17–22} Typically, M1 activation is not consistently found in every subject and, when present, is less intense than during motor execution of the same movement. The activated zone overlaps the zone activated during execution, with the same voxels involved in the two conditions.\textsuperscript{21} The involvement of M1 during motor imagery can also be detected with the magnetoencephalographic (MEG) technique: in this case, the activity of the motor cortex is inferred from a specific change in cortical activity (suppression of the 20-Hz rebound induced by a peripheral nerve stimulation), which is observed in the precentral gyrus during manipulative finger movements, during motor imagery of the same movements,\textsuperscript{23} and also during observation of an actor moving his fingers.\textsuperscript{24} These MEG findings represent a direct demonstration of the existence of a cortical system for matching execution, imagination, and observation of the same movements. (See also Reference 25.)

Experiments reporting activation of M1 during action representation (like those reporting increased corticospinal excitability; see below) fall under the critique that the observed changes might simply reveal incomplete inhibition of action or incomplete relaxation of motor activity during the mental process of imagination. In fact, this critique can be ruled out by other findings showing primary motor cortical activation during imagined movements in subjects with an amputated or a paralyzed limb. Ersland et al.\textsuperscript{26} found an increased metabolic activity in the contralateral primary motor cortex in a subject performing imaginary finger tapping with his amputated right hand. Lotze et al.\textsuperscript{7} found in amputees with impressions of phantom limbs that imagination of moving the phantom hand produced an activation of the contralateral motor and somatosensory cortex that was higher than that produced by imagination of hand movements in control subjects. Brugger et al.\textsuperscript{27} report the striking observation of a woman born without limbs, who presented strong sensations of phantom limbs. Although these sensations did not elicit activation of sensorimotor cortex (only premotor and parietal cortices were activated bilaterally), they were increased by stimulation of the sensorimotor cortex by TMS.

These observations raise a key question. Do motor images in amputees represent actions to the same extent that they do in normals, or are they real actions (i.e., if the muscles were still there or were still connected, would they contract)? This is an almost impossible question to answer. One could argue that the difference between the two situations is that motor images involve an inhibitory process, whereas blocked movements do not. Thus, in principle, one should be able to detect (by inspecting the activation pattern during a motor imagery task) whether the inhibitory process is present or not: if yes, this would mean that the subjects are generating a genuine motor image; if not, they are simply attempting to perform a movement in spite of the absence of the effector. In the latter case, however, one wonders why there should be an inhibitory process if there is no need to block the output.
The description of the (motor) brain activity during action representation strongly suggests that the same areas are involved during different types of representations. Consciously evoking a motor image, making an evaluation of the feasibility of a movement, or observing an action performed by somebody else — to name only those factors — results in closely similar activation patterns. In addition, this same activation pattern can also be recorded during execution of the corresponding action. In other words, the neural correlates of representing an action are shared by different types of representations. A dramatic illustration of this concept of shared representation is offered by the finding of mirror neurons. Mirror neurons were identified in the monkey premotor cortex. They are activated in two conditions: first, they fire when the animal is involved in a specific motor action, like picking a piece of food with a precision grip; second, they fire when the immobile animal watches the same action performed by an external agent (another monkey or an experimenter). In other words, mirror neurons represent one particular type of action, irrespective of the agent who performs it. At this point, it could be suspected that the signal produced by these neurons, and exploited by other elements downstream in the information processing flow, would be the same for an action performed by the self and by another agent: the two modalities of that action (executed and observed) would thus completely share the same neural representation. In fact, other premotor neurons (the canonical neurons), and presumably many other neuron populations as well, fire only when the monkey performs the action and not when it observes it from another agent. This is indeed another critical feature of the shared representations concept: they overlap only partially, and the part of a given representation that does not overlap can be the cue for attributing the action to the self or to another.

A mechanism similar to that of mirror neurons operates in humans. Brain activity during different conditions where subjects were self-representing actions (e.g., executing and imagining actions, inspecting tools, or observing actions performed by other people) was compared. The outcome of these studies is twofold. First, there exists a cortical network common to all conditions. As shown in the preceding section, the motor cortex is part of this network, which also includes cortical areas located in the superior and inferior parietal lobules, the ventral premotor cortex, and the supplementary motor area (SMA). Second, motor representations for each individual condition are clearly specified by the activation of cortical zones, which do not overlap between conditions.

9.4 CHANGES IN THE EXCITABILITY OF THE MOTOR PATHWAYS DURING MOTOR REPRESENTATIONS

Measuring the changes in the excitability of motor pathways during various forms of action representation can also provide further cues on the involved mechanisms. Indeed, it is a frequent finding that some degree of background electromyographic (EMG) activity persists in the muscular groups involved in the simulated action. This finding suggests that during, for example, motor imagery, motor commands to muscles are only partially blocked, and that motoneurons are close to the firing
threshold. Bonnet et al.\textsuperscript{40} confirmed this point by measuring spinal reflexes during motor imagery tasks. They instructed subjects either to press isometrically on a pedal, or to mentally simulate the same action. Two levels of strength (weak and strong) were used. The H-reflexes in response to direct electrical stimulation of the popliteous nerve and the T-reflexes in response to a tap on the soleus tendon were measured. Both types of reflexes were increased during mental simulation and this increase correlated with the force of the simulated pressure. (See also Reference 39.)

The excitability of the corticospinal pathway was also extensively tested in several experiments using TMS. This method permits one to measure the amplitude of motor-evoked potentials (MEPs) produced in the muscles involved in mental simulation of an action, by the magnetically induced electrical stimulus applied to the corresponding area of the contralateral motor cortex. Authors consistently found a specific increase of MEPs in those muscles involved in an imagined task — e.g., in the flexor muscles during imagination of hand closure — whereas no such increase was found in the antagonist extensor muscles.\textsuperscript{41–43} Not surprisingly, very similar results were obtained when MEPs were measured during the observation of actions. In this situation, where the subject is instructed simply to watch an actor, the MEP increase is also restricted to the muscle group involved in the observed action (e.g., the action of grasping an object\textsuperscript{44,45}). Interestingly, the effects of observation are not limited to the visual domain. Fadiga et al.\textsuperscript{46} were able to show that listening to specific phonemes increases the excitability of the motor pathway to the relevant tongue muscle. Finally, Baldissera et al.\textsuperscript{47} found changes in upper limb H-reflexes during observation of finger flexion or extension.

These results add support to the view of an involvement of the motor system during different types of mental representation of actions. Indeed, in a recent study, Clark et al.\textsuperscript{48} were able to compare MEP amplitude in the same subjects while explicitly imagining, observing, and physically executing the same hand gestures. They found that observation and imagery conditions led to a similar facilitation in MEP amplitude in the relevant hand muscle. In addition, during action observation, a condition of “active” observation (with the instruction to subsequently imitate) yielded larger MEPs than a purely passive observation. Although MEP facilitation was weaker during action representation than during physical execution of the same action, the finding clearly calls for a unitary mechanism based on action simulation. This point will be developed further in another section.

9.5 THE PROBLEM OF ACTION INHIBITION DURING THE REPRESENTATION OF ACTIONS

The comparison between the autonomic and the motor systems during action representation reveals that, whereas activation of the former leads to changes at the level of peripheral effectors, this is not the case for the latter, where the contraction of the involved muscles is inhibited. Considering the above body of data about the activity of the motor system during covert actions, there are two possible explanations for this absence of motor output. The first interpretation postulates that the transfer of the motor engrams elaborated within premotor or supramotor cortical
areas (e.g., the dorsal and ventral premotor cortices, the parietal cortex) to M1 would be blocked by a central inhibitory mechanism. The prefrontal cortical areas, which are found to be active during motor imagery, could represent a possible locus for this behavioral inhibition. An observation by Marshall et al. of a patient with a hysterical paralysis of the left side of the body lends support to this possibility. Although in this patient a normal activation (mapped with PET) of the left sensorimotor cortex was observed during movements of the right “good” leg, no such activation was observed on the right side during unsuccessful attempts to move the left “bad” leg. Instead, the right anterior cingulate and orbitofrontal cortices were significantly activated. This result suggests that these prefrontal areas exerted a state-dependent inhibition on the motor system when the intention to move the left leg was formed. This point was specifically investigated by Brass et al. in a neuroimaging experiment in normal subjects. Subjects were instructed to perform finger movements while they were observing another person executing either congruent or incongruent movements. When the observed movements were incongruent with respect to the instructed ones, the subjects had to inhibit their spontaneous tendency to imitate the movements of the other person. This task resulted in a strong activation of the dorsolateral and frontopolar areas of the prefrontal cortex. The hypothesis of a cortico-cortical “disconnection” is not compatible, however, with the simple fact that the motor cortex remains activated during action representation. A possible interpretation for the above data could be that the prefrontal cortex is involved, not in inhibiting the execution of represented actions, but rather in a process of selecting the appropriate representation. While executing an instructed action incompatible with an observed one, one has to select the endogenous representation and ignore the representation arising from the outside; in other words, one has to prevent oneself from being distracted by an external event.

In order to account for the empirical data showing the involvement of the motor cortex, we must conclude that the inhibitory mechanism is localized downstream of the motor cortex, possibly at the spinal cord or brainstem level. A tentative hypothesis would be that a dual mechanism operates at the spinal level. The subthreshold preparation to move, reflected by the increased corticospinal tract activity, would be paralleled by an inhibitory influence for suppressing the overt movement. The posterior cerebellum may play an important role in this inhibitory process. Whereas during action execution, the activated cerebellar areas are located in anterior and lateral regions, those activated during imagery and action observation are located in the posterior cerebellum. A similar explanation, but using a different site for inhibition, was put forward by Prut and Fetz to explain motor inhibition in the monkey while the animal is waiting for execution of a learned action. They showed that, during the waiting period where the monkey is ready to move, spinal interneurons are activated, hence indicating that the spinal motor network is being primed by the descending cortico-motoneuronal input. Because the overt movement was suppressed during this period, Prut and Fetz hypothesized a superimposed global inhibition, possibly originating in the premotor cortex, and propagating to the spinal cord, parallel to the excitatory input. This hypothesis would account for both the increased motoneuron excitability and the block of muscular activity during action representation.
9.6 THE SIMULATION HYPOTHESIS AND ITS IMPLICATIONS

The simulation hypothesis is a rather broad framework accounting for the relationship of mental phenomena to the activity of the neural substrate. Its empirical basis accumulated from experiments in cognitive neuroscience in the past two decades. One of the most influential results showed that visual mental images rely on activation of the early stages of information processing of the visual system. The primary visual cortex (V1) is consistently involved in visual mental imagery, with an additional selective involvement of the inferotemporal cortex during imagery of visual objects and of the occipitoparietal cortex in visual spatial imagery. The explanation put forward for an activation of low-level processing areas during a high-level cognitive activity is that activation of topographically organized areas, such as V1, is needed for replacing the image within a spatial frame of reference. Higher-order areas, because they lack topographical organization, would not be able, by themselves, to achieve this task. In other words, the processing of visual imagery would have to follow the same processing track as visual perception for giving an image its spatial layout, a process that requires the participation of V1.

This reasoning can be extended to the domain of action representations. The definition we gave at the beginning of this paper for represented actions is that they correspond to covert, quasi-executed actions, a definition that accounts for many of the properties of action representations that have been described here. Thus, by drawing a parallel with perceptual representations such as visual mental imagery, we come to the proposition that, if a represented action is a simulated action, then it should involve the mechanisms that normally participate in motor execution. In the above sections, we have seen a large amount of data that satisfy this proposition. Conversely, the content of motor images is explained by the involvement of neural structures such as M1, the premotor cortex, the basal ganglia, and the cerebellum, because this is where the aspects of action related to execution are normally processed. In other words, if the mental content of motor images is what it is, this is because the neural correlates include the structures required for execution. But this reasoning leads to another point, which can be set as a question: if motor images are not executed, why do they involve the activation of executive neural structures? The answer to this question can only be partial. The reason for this is that we do not know the precise function of all the activated neuron populations in these areas. Although some uncertainty remains, however, an answer can be given for those neurons that are connected to the spinal chord, the activation of which is responsible for the increased excitability at the motoneuron level that is observed during various types of action representation. During execution, these neurons are involved in selecting the proper muscular addresses for producing the action, for applying the required muscular force, for encoding the biomechanical limitations, for selecting the final endpoint postures, for optimizing the trajectory dynamics, and so on. Thus, by analogy with the activation of primary visual areas in visual mental imagery, which is thought to restore the topographical layout of the image, it could be proposed that M1 activation in motor representation is needed for providing the
represented action with its motor format. In other words, in order for a represented action to be felt as a real action, it needs to be framed according to the constraints of a real action.

This proposition seems even easier to fulfill for action representations originating from observed actions. In that case, the simulation must provide a frame to the perception of the action: the observer understands the action he sees to the extent he can simulate it. In order for the perception to be veridical, the simulation must be complete and must involve all the aspects of the observed action. A mere observation, without activation of the motor system, would only provide a description of the visible aspects of the movements of the agent, but it would not give precise information about the intrinsic components of the observed action which are critical for understanding what the action is about, what its goal is, and how to reproduce it.

9.7 IMPLICATIONS OF THE SIMULATION THEORY

9.7.1 Mental Training

The strong relationships of motor imagery to the neural substrate lead to the logical expectation that the central changes produced in the motor system during imagery should affect subsequent motor performance. The sport psychology literature in the early 1960s offers a large number of studies reporting measurable effects of mental imagery on subsequent motor performance. (For review and meta-analysis, see References 54, 55.) Mental training has been shown to affect several aspects of motor performance normally thought to be specific outcomes of physical training, such as the increase in strength of muscular contraction, improvement in movement speed, and reduction of variability and increase in temporal consistency of movements.

Several explanations for these phenomena have been proposed in the literature. One possibility is that mental training could modify a new perceptual organization or a new insight of the action to be performed. Alternatively, minimal movements occurring during mental training would be sufficient to generate proprioceptive feedback and reactivation kinesthetic images stored from previous movements. Still another possibility would be that visual imagery is involved in providing an abstract representational system of spatial information. (For a review of these explanations, see Reference 12.) Finally, the most logical explanation would be that the motor activation observed during mental training rehearses the motor pathways and facilitates execution. This explanation is strongly supported by experimental data. Pascual-Leone et al.11 used TMS to evaluate the changes in cortical excitability during mental training of finger movements. These authors found that the size of the excitable area devoted to the finger was increased as movements were repeated over training periods. The increase in the size of the excitable area produced by imaginal training was similar to that obtained during physical training. More recently, Lafleur et al.58 showed that learning a motor task by using motor imagery induces a pattern of dynamic changes in cortical activation similar to that occurring during physical practice. In both conditions, a first phase is observed, with increase in activity in the premotor cortex and the cerebellum. Subsequently, this activation tends to
disappear and to be replaced by activation in the basal ganglia and the prefrontal
cortex (in the orbitofrontal and anterior cingular regions).

The simulation interpretation of the effects of mental training is confirmed by
recent experimental evidence showing that subjects can learn to voluntarily increase
the degree of activation of their motor cortex during an imagined manual action.\cite{59}
Subjects first need to receive an ongoing information about the level of activation
during the training period. This information can be provided by monitoring a con-
tinuously updated fMRI signal taken from the cortical motor area. Subsequently,
subjects become able to increase the level of activation in their motor cortex without
recourse to the feedback signal. According to deCharms et al. this procedure yields
a level of activity in the somatomotor cortex that is similar to, or higher than, the
level of activity during actual manual action. Obviously, this type of result, showing
the possibility of increasing activity in a specific brain area at will, opens a number
of potential applications for designing new training techniques, not only in the
domain of action, but also in the realm of the control of behavior in general.
Rehabilitation procedures for motor impairments should greatly benefit from this
possibility.

9.7.2 **COUPLING MOTOR REPRESENTATIONS WITH NEURO-PROSTHETIC DEVICES**

Evidence has been provided that represented actions are simulated real actions. More
specifically, represented actions involve the orderly activation of the same neural
structures that would be involved if the action were actually executed (the definition
of action simulation). Following this line of thought, it seems logical that, if the
neural in the motor areas of a subject imagining a movement could be properly
monitored and connected to effectors, the imagined movement would become vis-
ible. This conjecture is the basis for building hybrid brain–machine interfaces that
could be used to control artificial devices, with the ambition to restore motor function
in patients with severe motor disabilities or paralysis.\cite{60,61} Recent work has shown
that a monkey can be trained to move a spot on a computer screen just by “thinking”
the displacement of the spot. In the experiment of Serruya et al.,\cite{62} the monkey was
implanted with an electrode for recording the activity of a small neuronal population
in area M1 controlling the animal’s arm movement. The monkey first used a manip-
ulandum for displacing a spot on the computer screen. Then the connection between
the manipulandum and the computer was replaced by a connection between the
output of the microelectrode and the spot: the monkey immediately used the neural-
activity-based signal to carry out the task without any further training. During this
time, the animal made intermittent arm movements, or no arm movements. The
importance of this finding is twofold. Not only does it show that nonhuman primates,
like humans, can generate motor representations that have properties similar to real
actions; it is also of a high potential value for designing rehabilitation procedures.
As already mentioned, the ability of human subjects to learn to increase their cortical
activity at will indicates that it will become possible, for example, to train patients
to learn to activate neuro-prosthetic devices and to recover in this way part of their
motor autonomy.
9.7.3 Learning by Observation and Imitation

There is a wealth of data in the literature showing that observing a movement facilitates the execution of that movement by the observer. Brass et al.,\textsuperscript{63} for example, noticed that the execution of instructed finger movements is influenced by the observation of another person performing compatible or incompatible finger movements. If the movements performed by the observer are compatible with those performed by the other person, they are clearly facilitated (e.g., their reaction time is shorter). Conversely, incompatibility of the movements of the observer with those of the other person yields to degraded performance. (See also Reference 64.) Craigero et al.\textsuperscript{65} also found that observing pictures showing hand postures facilitates the execution of a grasping hand movement when the observed posture is congruent with the executed movement. These data stress the point that observing the performance of another person facilitates the formation of effector-specific motor representations.

According to Sebanz et al.,\textsuperscript{66} simply observing the action at the disposal of another person creates in the observer a representation of that action: this representation will facilitate the execution of the action by the observer. As for the action representation created during motor imagery, those that result from action observation seem to include information related to action execution. This is suggested by a series of experiments by Knoblich and his coworkers. Knoblich and Flach\textsuperscript{67} presented subjects with videos of an action (throwing darts) that these subjects had previously performed and videos of the same action performed by other subjects. The subject’s task consisted of predicting the accuracy of the observed actions. Prediction was more accurate when subjects observed their own actions than when they observed another person’s actions. Thus, the observation of self-generated actions is more informative, because the mechanism that simulates the observed action is the same as that which produced it. These data represent a basis for the widespread phenomenon of learning by observation. Heyes and Foster,\textsuperscript{68} for example, found that subjects simply watching an experimenter performing a sequence of movements can learn the sequence as efficiently as when practicing the task themselves.

These findings may have interesting implications in the domain of pathology. In patients with limb amputation or denervation, the activity of the corresponding part of the motor cortex tends to decrease over time. At the same time, the patients may experience subjective phenomena such as phantom limb or phantom pain. As already mentioned in the section on cortical plasticity, Giraux and Sirigu,\textsuperscript{9} in two such patients with a unilateral brachial plexus avulsion, showed that a normal activity could be restored in their motor cortices by means of observational training. These patients were trained in a situation where the image of the valid hand was visually transposed (by way of mirrors; see Reference 69) at the location of the impaired hand. They were instructed to move the valid hand that they could see at the place of the impaired arm. Following a series of 24 daily visuomotor training sessions, the activity of the M1 area contralateral to the impaired (paralyzed) arm, monitored by fMRI, was greatly increased. This result shows that observation of a normally moving limb can activate the motor area controlling the homologous limb in the observer. A possible explanation for this phenomenon is that mirror neurons similar to those found in the monkey premotor cortex are activated by observation of the
moving hand and trigger the activity of M1 neurons innervating the impaired hand. In these two patients, this visuomotor training procedure had a beneficial effect, not in improving their hand movements, which remained impaired due to the plexus brachial lesion, but in decreasing their phantom limb pain. This effect suggests that the motor cortex, in addition to its role in controlling movements, may also influence the processing of sensory input arising from the effector it controls.

The ability of human subjects to imitate each other derives from the possibility of forming action representations from the observation of other people. Neuro-imaging studies of imitation in humans tend to favor what Iacoboni et al. call the direct matching hypothesis. According to this hypothesis, brain areas that become active during execution of a movement should become more active when that movement is elicited by the observation of an identical movement made by another person. Areas in the left inferior frontal cortex and in the parietal cortex seem to fulfill this requirement. This result, showing that brain areas for execution and observation of a movement are matched, is compatible with the simulation theory. Furthermore, it raises again the point (already raised in the section about shared representations) of how two different representations of the same action are disentangled from one another. Other studies dealing with imitation suggest that areas might be activated differently whether an action is internally produced or generated by another agent.

9.8 CONCLUSION: THE ROLE OF SIMULATION IN MOTOR COGNITION

The above pattern of results on the mechanisms of covert action corresponds to the central stages of action organization, uncontaminated by the effects of execution. As such, it represents a possible framework for motor cognition.

First, because all aspects of action appear to be involved during action representation, it seems a logical consequence of this rehearsal of the corresponding brain structures, and specifically the motor structures, that the subsequent execution will be facilitated. The presence of activity in the motor system during covert action puts the action representation in a true motor format, so that it can be regarded by the motor system as a real action. This facilitation explains various forms of training (e.g., mental training) and learning (e.g., observational learning) which occur as a consequence of self-representing an action. In addition, imitation seems to be based on directly matching the observed action onto an internal simulation of that action.

Second, activation of the motor cortex and of the descending motor pathway seems to fulfill several critical functions. First, this activation contributes to generating corollary signals that propagate upstream to the parietal and premotor cortices. This mechanism would allow for evaluating the potential consequences of the future action. (See Reference 72 for description of a control model that accounts for this function.) It could also provide the subject with information for consciously monitoring his S-states and realizing that he is the agent of this covert activity, in spite of the absence of overt behavior.
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