

Human motor cortex excitability during the perception of others' action

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Neuroscience research during the past ten years has fundamentally changed the traditional view of the motor system. In monkeys, the finding that premotor neurons also discharge during visual stimulation (visuomotor neurons) raises new hypotheses about the putative role played by motor representations in perceptual functions. Among visuomotor neurons, mirror neurons might be involved in understanding the actions of others and might, therefore, be crucial in interindividual communication. Functional brain imaging studies enabled us to localize the human mirror system, but the demonstration that the motor cortex dynamically replicates the observed actions, as if they were executed by the observer, can only be given by fast and focal measurements of cortical activity. Transcranial magnetic stimulation enables us to instantaneously estimate corticospinal excitability, and has been used to study the human mirror system at work during the perception of actions performed by other individuals. In the past ten years several TMS experiments have been performed investigating the involvement of motor system during others' action observation. Results suggest that when we observe another individual acting we strongly 'resonate' with his or her action. In other words, our motor system simulates underthreshold the observed action in a strictly congruent fashion. The involved muscles are the same as those used in the observed action and their activation is temporally strictly coupled with the dynamics of the observed action.

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Introduction

A large amount of evidence suggests that actions are represented in the brain in a similar way to words in a vocabulary [1]. Neurophysiological studies of monkey premotor cortex have established that hand and mouth goal directed actions are represented in area F5. This

goal-directed encoding is demonstrated by the discriminative behavior of F5 neurons when an action that is motorically similar to the one effective in triggering neuronal response is executed in a different context. For instance, a F5 neuron that responds during hand grasping will not respond when similar finger movements are performed with a different purpose, for example, scratching [2]. Several F5 neurons, in addition to their motor properties, also respond to visual stimuli. Mirror neurons form a class of visuomotor neurons that respond both when the monkey performs goal-directed hand actions and when it observes other individuals performing similar actions [3–5].

Prompted by the discovery of monkey mirror neurons and stimulated by their possible involvement in high-level cognitive functions, such as understanding others' behavior and interindividual communication, several functional brain imaging studies were performed to investigate whether or not a mirror-neuron system is also present in the human brain. Results showed that observation of an action recruits a consistent network of cortical areas, including the ventral premotor cortex (which extends posteriorly to the primary motor cortex), the inferior frontal gyrus, the inferior parietal lobule and the superior temporal cortex (for recent literature see Rizzolatti and Craighero [6]). However, brain imaging studies give us a static picture of the activated areas and do not enable us to conclude that the observer's motor system is dynamically (on-line) replicating the observed movements. Transcranial magnetic stimulation (TMS) can be used to measure the corticospinal (CS) excitability with a relatively high temporal resolution, and has been used extensively to address this issue.

Here, we review the most recent studies that investigate using TMS how the human motor cortex reacts to other's action observation.

Transcranial magnetic stimulation: a tool to measure motor activation during observation of others' actions

Although TMS was originally designed to test the integrity of the CS system by recording a motor evoked potential (MEP) from a given muscle in response to primary motor cortex (M1) stimulation, the potential of TMS to investigate brain functions has proved much greater. TMS can be used either to inactivate specific brain regions, by repetitively stimulating the brain to obtain long lasting inhibition, or to interfere transiently with its neural activity, by applying a single TMS pulse

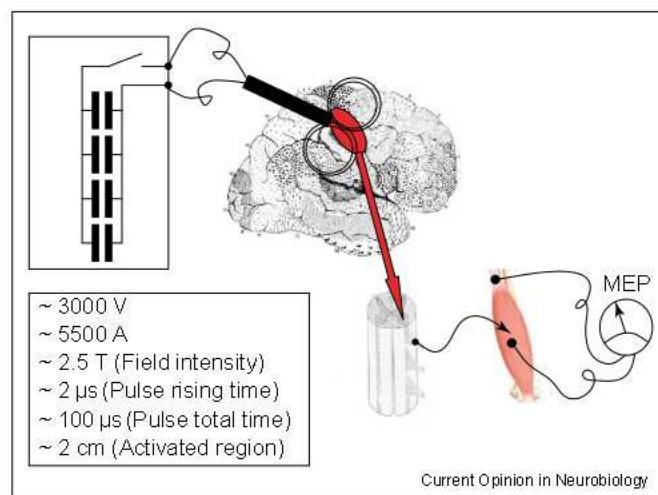
[7,8]. This approach enables us to infer the contribution of the 'perturbed' area to the investigated function, similar to the situation in animal experiments in which muscimol injections enable us to deduce the role of the inactivated structure by quantifying the induced behavioral deficit [9,10]. The precision of localization of the TMS target has also been recently greatly improved by using frameless stereotaxic methods (for recent literature, see Noïrhomme *et al.* [11•]), enabling us to target more precisely those 'motorically silent' cortical regions lying outside M1. In addition to its use in inactivation studies, TMS can also be used to monitor changes in CS excitability that specifically accompany motor performance [12], or that are induced by the activity of various brain regions connected with M1. This can be done by measuring the amplitude of MEPs elicited by TMS under various experimental conditions (see Figure 1).

The first evidence that CS excitability is modulated during observation of an action was given by our group ten years ago [13]. TMS was applied to the area of motor cortex that represents the hand and MEPs were recorded from contralateral hand muscles (extensor digitorum communis [EDC], flexor digitorum superficialis [FDS], first dorsal interosseus [FDI], and opponens pollicis [OP]) during observation of transitive (grasping of different objects) and intransitive (arm elevation) arm-hand movements. During observation of grasping action, the amplitude of MEPs recorded from OP and FDI increased compared with those observed in the control conditions. During observation of arm movement the increase was present in all muscles except OP (Figure 2c).

This experimental outcome raised the question of whether the muscles that were facilitated during the

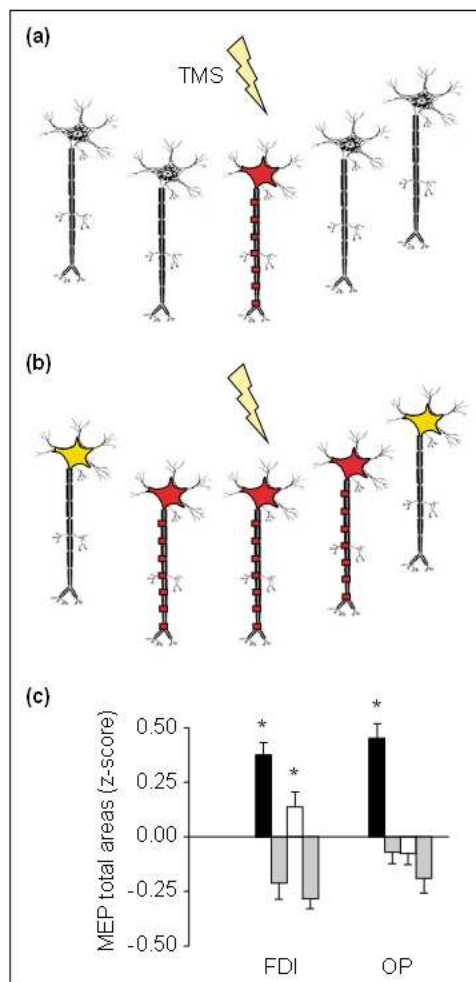
observation of a given action were the same as those active during its execution. To answer this question, EMG from hand muscles was recorded during rest, object grasping and arm lifting movements, and the pattern of EMG activation replicated exactly that of MEPs elicited by TMS during action observation. These results have been successfully replicated and extended by other groups. Brighina *et al.* [14] investigated the effect of the observation of simple intransitive thumb movements (abduction) and of sequential thumb–finger opposition movements on left and right motor cortex excitability. Although some methodological details are absent from the paper (e.g. whether the presented action was performed by a right or a left hand), the results show an increase of the CS excitability in both hemispheres that depended on the complexity of the observed task. More recently, Gangitano *et al.* [15] showed the presence of a strict temporal coupling between the changes in CS excitability and the dynamics of the observed action. Indeed, MEPs recorded from the FDI muscle at different time intervals during passive observation of a pincer grasping action matched in time the dynamics of the kinematics of the pinch that characterized the actual movements. Clark *et al.* [16•] have recently assessed the specificity of the CS facilitation induced by action observation. They recorded MEPs from FDI muscle of the dominant hand during TMS of contralateral M1 while participants first, merely observed, second, imagined, or third, observed to subsequently imitate simple hand actions. They did not find any statistically significant difference among the three conditions. However, MEPs recorded during these three conditions were strongly facilitated when compared with those recorded during highly demanding non-motor cognitive tasks (i.e. MEPS collected during a backwards mental counting task).

Figure 1



Transcranial magnetic stimulation. The fast circulation of a strong electrical current in the coil positioned on the skull induces an electric current in the brain. If the induced current is large enough, underlying cortical neurons are brought over threshold and the descending volley reaches the spinal motoneurons, evoking a MEP detectable by standard electromyography techniques.

Figure 2



Transcranial magnetic stimulation can be used to instantaneously measure the excitability of the CS system. Schematic depiction of the effect of a same intensity TMS on (a) resting and (b) underthreshold depolarized (note the yellow soma) CS neurons. In (c) typical changes of corticospinal excitability during action observation are shown. Bar histograms describe the effect of hand grasping observation (black bars), arm movement observation (white bars) and control condition (shaded bars) on the TMS-induced MEPs recorded from first dorsal interosseus (FDI) and opponens pollicis (OP) muscles (modified with permission from Fadiga et al. [13]).

There are at least two possible explanations for the origin of the MEP facilitation induced by action observation. The first one is that the facilitation of MEPs is due to the enhancement of M1 excitability produced through excitatory cortico-cortical connections. Considering that monkey area F5, where mirror neurons are located, is premotor cortex that is strongly connected with M1 [17], one could explain the facilitation of MEPs induced by action observation as the consequence of a facilitatory cortico-cortical effect arising from the human homolog of monkey area F5. The second possible explanation is that TMS reveals, through the CS

Glossary

H-reflex: Hoffmann reflex, its amplitude (as recorded by EMG, electromyography) depends upon spinal motoneuron excitability, and it is evoked by stimulating the afferent fibers in peripheral nerves.

F-wave: Centrifugal discharge recorded by EMG and evoked in motoneurons by antidromic excitation of the motoneuron axon-soma.

descending volley, a facilitation of motoneurons (MNs) mediated by parallel pathways (e.g. from the premotor cortex to the brainstem). Indeed, when MEP amplitude variation is used as an end-point measure, a change in M1 excitability cannot be firmly established unless any modification in MN excitability is ruled out. Furthermore, changes in MEP amplitude caused by a variation of M1 or MN excitability are undistinguishable and, unfortunately, techniques that enable us to address this issue are uncomfortable for subjects (transcranial electrical stimulation, brainstem electrical stimulation), inapplicable (as in the case of H-reflex for intrinsic hand muscles), or unreliable because they assess only a small fraction of the whole MN population (as in the case of F-wave).

To assess the spinal involvement in action observation-related MEP facilitation, Baldissera *et al.* [18] investigated spinal cord excitability during action viewing. To do this, they measured the amplitude of H-reflex (see glossary) in finger flexor forearm muscles while subjects were looking at goal-directed hand actions. Results showed that although there was a significant modulation of the H-reflex specifically related to the different phases of the observed movement, the modulation pattern was opposite to that occurring at the cortical level. Whereas modulation of cortical excitability strictly mimics the seen movements, as if they were performed by the observer, the spinal cord excitability appears to be reciprocally modulated. Indeed, the spinal MNs of finger flexors were facilitated during observation of hand opening (finger extension) but inhibited during observation of hand closure (finger flexion). This effect was interpreted as the expression of a mechanism serving to block overt execution of seen actions. However, other authors failed in showing specific changes in H-reflex amplitude during observation of simple finger movements (see below; [19]).

The more recently developed paired-pulse TMS might help to determine the cortical or spinal origin of CS facilitation (see [20]). The rationale of this technique is the use of a subthreshold conditioning TMS pulse followed, at various delays, by a supra-threshold TMS test pulse. Depending on the delay between these two pulses, it is possible to investigate changes in the excitability of excitatory or inhibitory interneurons within M1 itself. Intracortical inhibition (ICI) is usually observed for short (1–5 ms) or long (50–200 ms) intervals between conditioning and test TMS, whereas intracortical

facilitation (ICF) was maximal for 8–20 ms intervals. Strafella and Paus [21] used this approach to examine changes in cortical excitability during action observation. They stimulated the left M1 during rest, observation of handwriting and observation of arm movements. MEPs were recorded from the FDI and biceps brachialis muscles. Results showed that action observation induced a facilitation of MEP amplitude evoked by the single test stimulus and led to a decreased ICI at 3 ms interstimulus interval. The authors, therefore, came to the conclusion that CS facilitation induced by action observation was attributable to cortico–cortical facilitating connections.

A series of experiments was set up with the aim of clarifying the modulation of CS excitability induced by some peculiar characteristics of the observed action. In a recent experiment aiming to investigate whether human mirror neurons are somehow tuned for one's own actions or not, Patuzzo *et al.* [19] showed an increase in right FDS MEP amplitude associated with a reduction in ICI, during the observation of both self (pre-recorded videos representing subjects' own motor performance) and non-self finger flexion, as compared with those at rest. Moreover, these authors failed to observe significant changes in spinal excitability as tested with H-reflex or F-wave (see glossary). Maeda *et al.* [22] investigated the self–others issue extensively, by using TMS to measure CS excitability during observation of actions of various degrees of familiarity. In two conditions, subjects were watching their own previously recorded hand actions. In the 'frequently observed configuration' the acting fingers were directed away from the body, and in the 'not frequently observed configuration' the fingers were directed toward the body. In the remaining two conditions, subjects were watching the previously recorded hand actions of unknown people both in the frequently (fingers toward the body) and in the not frequently (fingers away from the body) configuration. Results showed that the frequently observed hand actions produced greater CS excitability with respect to the control condition, whereas this was not the case for the less frequently observed hand actions. In a subsequent experiment, Maeda *et al.* [23] further investigated the issue of the orientation of the observed hand. Results showed that MEP facilitation was greater during observation of natural hand orientations. Aziz-Zadeh *et al.* [24] investigated whether CS facilitation during action observation is modulated by the laterality of the observed body part or not, and they found that when TMS was applied over the left M1, MEPs were larger while observing right hand actions. Likewise, when TMS was applied over the right M1, MEPs were larger while observing left hand actions.

Finally, in a very recent experiment, Gangitano *et al.* [25**] investigated the reason behind the presence of a

strict temporal coupling between the CS excitability modulation and the dynamics of an observed reaching–grasping movement (see Gangitano *et al.* [15]). Two sets of visual stimuli were presented in two distinct experiments. The first stimulus was a video-clip showing a natural reaching–grasping movement. The second video-clip represented an anomalous movement, in which the temporal coupling between reaching and grasping components was disrupted by changing the time of occurrence of the maximal finger aperture. This effect was realized either by keeping the hand closed throughout the whole reaching and opening it just in proximity to the target (Experiment 1) or by substituting part of the natural finger opening with a sudden movement of closure (Experiment 2). Whereas in Experiment 1 MEP modulation was generally absent, the observation of video-clip presented in Experiment 2 induced a clear, significant modulation of CS excitability. This modulation, however, was limited to the part of the observed action preceding the visual perturbation (the sudden finger closure). These results suggest that any modification of the canonical plan of an observed action induces a reset of the mirror system, which therefore stops its activity. It can be deduced that the mirror system works online to predict the goal and the outcome of the observed action.

Motor facilitation induced by 'listening' to others' actions: a link with speech perception?

Others' actions do not generate only visually perceivable signals. Action-generated sounds and noises are also very common in nature. One might expect, therefore, that also this sensory information, related to a particular action, could determine motor activation specific for that same action. Very recently, it has been reported that a fraction of monkey mirror neurons, in addition to their visual response, also become active when the monkey listens to an action-related sound (e.g. breaking of a peanut) [26**]. It is tempting, therefore, to conclude that mirror neurons might form a multimodal representation of goal directed actions involved in action recognition. Experimental evidence shows similar results in humans. Aziz-Zadeh *et al.* [27] used TMS to explore whether or not CS excitability is modulated by listening to action-related sounds. In their experiment, left and right M1 were studied. MEPs were recorded from the contralateral FDI muscle while subjects listened to one of two kinds of bimanual hand action sounds (typing or tearing paper), to a bipedal leg action sound (walking) and to a control sound (thunder). Results showed that sounds associated with bimanual actions produced greater CS excitability than sounds associated with leg movements or control sounds. Moreover, this facilitation was exclusively lateralized to the left hemisphere.

Sundara *et al.* [28] tested the possibility that a mirror mechanism, similar to that found during observation of

actions, would also be present during presentation of speech gestures both in the visual and in the auditory modalities. The authors found that visual observation of speech movement enhanced MEP amplitude specifically in facial muscles involved in production of the observed speech. By contrast, listening to the sound did not produce MEP enhancement. This negative result, as far as speech sounds are concerned, might be explained by the fact that they recorded MEPs from muscles (facial) not directly involved in speech sound production. Indeed, our group [29] demonstrated that during speech listening there is an increase of MEP recorded from the listeners' tongue muscles when the presented words would strongly involve, when pronounced, tongue movements. Furthermore, the effect was stronger in the case of words than in the case of pseudowords, suggesting a possible unspecific facilitation of the motor speech center due to recognition that the presented material belongs to an extant word. As suggested by the 'motor theory of speech perception' originally proposed by A. Liberman [30], the presence of a phonetic resonance in the motor speech centers might subserve speech perception. This theory maintains that the ultimate constituents of speech are not sounds but articulatory gestures that have evolved exclusively at the service of language. According to Liberman's theory, the listener understands the speaker when his or her articulatory gesture representations are activated by the listening to verbal sounds. Also in this line is the study by Watkins et al. [31] demonstrating that speech perception, either by listening to speech or by observing speech-related lip movements, enhanced MEPs recorded from the orbicularis oris muscle of the lips. This increase in motor excitability during speech perception was, however, evident for left hemisphere stimulation only. In a subsequent experiment, Watkins and Paus [32^{••}] combined TMS with positron emission tomography to identify the brain regions mediating the changes in motor excitability during speech perception. Results showed that during auditory perception of speech, the increased size of the MEP obtained by stimulation over the face representation of the primary motor cortex correlated with regional increase of blood flow in the posterior part of the left inferior frontal gyrus (Broca's area). To verify the presence of an evolutionary link between the hand motor and the language system, as proposed by an influential theory of the evolution of communication [33], Floel et al. [34[•]] examined if, and to what extent, language activates the hand motor system. They recorded MEPs from the FDI muscle while subjects underwent three consecutive experiments attempting to isolate the components (articulatory linguistic, auditory, cognitive and visuospatial attentional) more crucial in activating the motor system. Results showed that productive and receptive linguistic tasks only excite the motor cortices for both hands.

Conclusions

A large body of evidence supports the view that perception of others' actions is constantly accompanied by motor facilitation of the observer's CS system. This facilitation is not only present during action observation but also while listening to action-related sounds and, more interestingly, while listening to speech. Further research is, however, necessary to investigate if the cytoarchitectonic homologies linking Broca's area — and particularly Brodmann's area 44 — to monkey's area F5, where mirror neurons have been found [35], might reflect the evolutionary continuity of a communicative system originally developed in our ancestors.

When considering TMS experiments, one should be aware of the fact that any change in CS excitability, even if a spinal contribution is firmly excluded, does not tell us much about the actual brain structures underlying the facilitation. Indeed, given the large number of non-primary motor areas that establish excitatory connections with M1, a change in M1 excitability could originate from any of these areas. However, the combination of TMS experiments with brain imaging studies represents a new powerful method of analysis. This new potential, together with the technical improvements of TMS technique (i.e. paired pulse stimulation, enhanced focalization and use of frameless stereotaxic systems), is expected to increase our working knowledge of the complex functions of the human motor system.

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