SHORT COMMUNICATION
Modulation of spinal excitability during observation of hand actions in humans

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Keywords: action observation, grasping, H-reflex, reaching movement

Abstract
There is growing evidence that observation of actions performed by other individuals activates observer’s cortical motor areas. This matching of observed actions on the observer’s motor repertoire could be at the basis of action recognition. Here we investigated if action observation, in addition to cortical motor areas, involves also low level motor structures mimicking the observed actions as if they were performed by the observer. Spinal cord excitability was tested by eliciting the H-reflex in a finger flexor muscle (flexor digitorum superficialis) in humans looking at goal-directed hand actions presented on a TV screen. We found that, in the absence of any detectable muscle activity, there was in the observers a significant modulation of the monosynaptic reflex size, specifically related to the different phases of the observed movement. The recorded H-reflex rapidly increased in size during hand opening, it was depressed during hand closing and quickly recovered during object lifting. This modulation pattern is, however, opposite to that occurring when the recorded muscles are actually executing the observed action [Lemon et al. (1995) J. Neurosci., 15, 6145±56]. Considering that, when investigated at cortical level the modulation pattern of corticospinal excitability replicates the observed movements [Fadiga et al. (1995) J. Neurophysiol., 73, 2608±2611], this spinal ‘inverted mirror’ behaviour might be finalised to prevent the overt replica of the seen action.

Introduction
A common clinical observation is that some patients with lesions involving frontal regions of the brain are compelled to mimic actions that other individuals make in front of them. This behaviour was formally described as ‘imitation behaviour’ by Lhermitte et al. (1986). In some circumstances, even normal individuals show behaviours similar to that of Lhermitte’s patients, for example lip mobilisation during attentive listening of speech, mouth opening of a mother feeding her baby, leg motion in spectators of sporting events. Moreover, in the newborn, visual presentation of mouth actions evokes a series of imitative movements, a phenomenon which disappears after a few weeks from birth (Meltzoff & Moore, 1977). All these phenomena suggest that, during observation of actions made by others, some sort of motor-resonance occurs in the observer.

The first experimental evidence favouring the existence of a motor-resonant system dependent on action observation, comes from single neuron recordings in the monkey’s ventral premotor cortex (Di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996a). Neurons of this region (area F5, Matelli et al., 1985) discharge both during preparation-execution of goal-directed hand actions and when the monkey observes similar actions performed by other individuals (mirror neurons, Gallese et al., 1996). Electrophysiological and brain imaging studies have recently shown that a similar motor-resonant mechanism also exists in humans. Electroencephalographic (Lelord et al., 1998) and magnetoencephalographic studies (Hari et al., 1998) showed that during action-viewing there is a desynchronization of cortical rhythms in the perirolandic derivations of the skull. Positron emission tomography (Grafton et al., 1996; Rizzolatti et al., 1996b; Decety et al., 1997; Grézes et al., 1998) and functional magnetic resonance (Binkofski et al., 1999), demonstrated that observation of actions activates Broca’s region plus, in some cases, a sector of the human ventral premotor cortex. The existence, both in monkeys and in humans, of a motor-resonant ‘mirror’ system suggests that such a system can play an important role in action imitation and, possibly, in action understanding (Jeannerod, 1994; Rizzolatti et al., 1996b; Gallese & Goldman, 1998). From the perspective that the observation of a specific action would activate in the observer the same neural substrate involved in the execution of that action, Fadiga et al. (1995) investigated the corticospinal excitability in humans observing other’s actions. They found that motor-evoked potentials (MEPs) in finger flexor muscles elicited in the observer by transcranial magnetic stimulation (TMS), were strongly facilitated during observation of other people closing their fingers on an object. This facilitation of MEPs can be due to the enhancement of primary motor cortex excitability produced through excitatory corticocortical connections from the putative human analogue of monkey area F5. Alternatively, it can be due to facilitatory outputs from the same ‘human F5’ area directed to the spinal cord. Although the corticocortical mechanism seems to be the most probable (recently suggested by Strafella & Paus, 2000), in the case of a direct influence of the premotor cortex on the spinal cord, the corticospinal volley elicited by the TMS of the

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Received 31 July 2000, revised 17 October 2000, accepted 19 October 2000
motor cortex would reveal a facilitation already present at the spinal level. The aim of the present study was to assess the modulation of spinal cord excitability during action viewing.

Materials and methods

General procedures

Human subjects took part in the experiments after having given their informed consent. The Local Ethical Committee approved the experimental procedures. All subjects were right-handed and had normal or corrected-normal visual acuity. During experiments, subjects sat in a comfortable armchair at a distance of 2 m from a 24-inch TV screen. Constant current pulses (duration 0.5 ms) were used to evoke the monosynaptic H-reflex in the right-hand finger flexor muscles. Bipolar surface stimulating electrodes (1.5 cm² silver plates) were positioned over the median nerve in the right cubital fossa, while surface the electromyogram was recorded by nonpolarizable disk electrodes (0.9 cm diameter) placed over the flexor digitorum superficialis (FDS) muscle. Care was paid to select a position on the median nerve from which an H-reflex confined to finger flexors was evoked. The correct position of the stimulating electrodes was assessed by visually inspecting the muscle twitches evoked by the stimulation. Stimulation intensity was always adjusted to elicit an H-reflex of about 10% of the maximum motor response (M wave) evoked by direct stimulation of the motor axons and care was taken to maintain a minimal and constant M wave during the whole session. During the experiments, subjects passively looked at video clips presented on the TV screen. During video presentation, subjects were requested to keep a still position and to view attentively what was presented on the screen. In order to assess the absence of any spontaneous EMG activity during video presentation, pretrigger background EMG (50 ms) was acquired before each H-reflex stimulation. No activity was found in the rectified background traces.

Experiment 1

Six subjects (3 males and 3 females, mean age 32 years, age range 23–60 years) were presented with a randomised sequence of three videos (video duration, 1000 ms) representing: (a) right-hand closing on a sphere (5 cm in diameter) with a whole hand prehension; (b) right-hand enlarging a rubber band with all fingertips; (c) right-hand at rest. Videos (a) and (b) presented movements during which the FDS muscle acts as an agonist and antagonist, respectively. Video (c) was used as a control. Hands were showed on the TV screen in natural dimensions.

During presentation of both hand opening (video a) and hand closing (video b), the test H-reflex was elicited, in a randomised sequence, after 25% (early stimulation) or 75% (late stimulation) of the total movement time. For the control condition, H-reflexes were elicited after 50% of the total image presentation time. For each of the five conditions (early opening, late opening, early closing, late closing and hand at rest), at least 30 H-reflexes were elicited.

In order to reduce background variability, the amplitude of each H-reflex response was expressed, for each subject, in terms of the difference (in μV) from the mean amplitude of all H-reflexes measured in that subject. Each movement condition was then compared with the control by using the t-test performed on paired data from each subject. The significance level was set at \( P < 0.05 \).
Results

Experiment 1

Figure 1 illustrates the effect of watching hand opening and hand closing movements, on the amplitude of H-reflex elicited in FDS muscle. During finger extension, the FDS H-reflex was consistently greater than the mean reflex size (ordinate 0). Facilitation was larger in the early phase than in the late phase. During finger closing, the H-reflex size was smaller than the mean reflex size. The maximum effect occurred in the late closing phase. When comparing the H-reflex excitability during movement observation, with that measured in the control situation, a significant difference \((P < 0.05)\) was found both for the early opening phase and the late closing phase. Late opening and early closing phases did not differ from control but were statistically different one from each other.

Experiment 2

The time course of the changes in H-reflex excitability during observation of a reaching–grasping–lifting sequence is illustrated in Fig. 2. The observer’s FDS H-reflex undergoes a complex modulation. H-reflex increased during observation of the finger opening, preceding grasping, and was progressively depressed during observation of finger closure on the object. Depression reached a maximum just after the finger contact with the sphere. During lifting, the H-reflex depression was quickly reverted to a second phase of facilitation.

ANOVA performed on the delays’ data (subjects: 9; factor: time; levels: 15 delays) showed the significance of the effect \(F_{14,98} = 8.58; P < 0.001\). The significance of the difference between each delay and control (delay 0) is indicated by asterisks in Fig. 2. Moreover, a significant difference \((P < 0.05)\) was found when each of the three H-reflexes, recorded during hand opening, were compared with each of the three H-reflexes recorded during the last part of hand closing.

In order to assess with more confidence the specificity of the observed effect, three out of the nine subjects were asked to look at videos reproducing a reaching–grasping–lifting movement performed at a faster speed (movement duration 800 ms). Also in this case (see Table 1), the changes in the H-reflex amplitude were correlated with the different phases of the observed movement with a pattern similar to that measured in Experiment 2 (facilitation during early hand opening; depression during hand closing and removal of depression during lifting).

Discussion

The results of the present study show that, in the absence of any detectable muscle activity, the mere observation of hand action modulates the excitability of the observer’s spinal circuitry involved in hand movement execution. The changes in the H-reflex size showed a very specific temporal correlation with the different phases of the observed movement. This effect was also replicated when subjects were presented with videos representing faster reaching–grasping movements. These data indicates that spinal circuits close to the final common path, or the alpha motoneurons themselves, are subliminally recruited during movement observation in a dynamic and specific way.
Movement duration was 800 ms. The H-reflex was tested at different delays from the video onset (as indicated in the Table). Each column reports the mean value (± SEM) of H-reflex modulation recorded from 3 subjects.

<table>
<thead>
<tr>
<th>H-reflex modulation (µV)</th>
<th>Early opening (delay 80 ms)</th>
<th>Late opening (delay 240 ms)</th>
<th>Hand closing (delay 400 ms)</th>
<th>Object grip (delay 600 ms)</th>
<th>Object lifting (delay 760 ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>42 ± 21</td>
<td>-25 ± 11</td>
<td>-20 ± 15</td>
<td>-73 ± 25</td>
<td>-38 ± 26</td>
</tr>
</tbody>
</table>

Although these data are interesting per se because they demonstrate the existence at the spinal level of a motor-resonant mechanism induced by action viewing, the excitability modulation observed during spinal H-reflex testing contrasts with the results obtained by Fadiga et al. (1995) with TMS of motor cortex during observation of hand actions similar to those used in the present experiment. While modulation of cortical excitability strictly mimics the seen movements as if they were performed by the observer (FDS MEPs enhancement during observation of hand closing), the spinal cord behaviour appears to be the opposite, being spinal motoneurons of finger flexors facilitated during observation of hand opening (finger extension) and inhibited during observation of hand closure (finger flexion). This discrepancy between the cortical and spinal behaviours during action observation can be explained by at least two different interpretations.

According to the first interpretation the ‘inverted’ spinal behaviour could reflect the existence of a mechanism related to what would happen at the spinal level during execution of the observed action. If this is true, execution and observation share also at the spinal level the same functional logic. At a first sight the action-observation-induced spinal modulation behaves in a way reciprocal to the natural role played by FDS muscle during reaching–grasping execution (see Lemon et al., 1995). One possible explanation of this paradoxical finding might be that the H-reflex, or a major component of it, was elicited in wrist rather than finger flexors. As a matter of fact, wrist flexors can be activated during finger extension in order to stabilize wrist posture (Humphrey, 1986). Because of the wide divergence of median 1a afferents, this possibility cannot be excluded despite the great care always paid to select a stimulation site from where the H-reflex was confined to finger flexors. Note, however, that finger closing on an object is always accompanied by a certain degree of wrist flexion. For this reason, the H-reflex inhibition we measured during observation of hand closing is strongly against the wrist interpretation. A second possible explanation is that motor-resonance of Ia presynaptic terminals instead of motoneurons (Carpenter et al., 1963). One can argue that, to recruit flexor motoneurons by the descending excitatory command without interference of the stretch reflex, their Ia input might be temporarily suppressed during the flexor phase by means of presynaptic inhibition. This interpretation, however, can plausibly explain the H-reflex size depression measured during observation of finger flexion but hardly justify the H-reflex facilitation during observation of finger extension.

According to the second interpretation, the spinal modulation occurring during action viewing is specifically related to motor-resonant mechanisms. A specific spinal mechanism is evoked, possibly trough descending projections originating in the human analogue of monkey premotor area F5. According to this view, premotor ‘human F5’ acts differently at the cortical and spinal levels. Premotor originating corticocortical connections modulate the corticospinal excitability in a way congruent with the observed movement, while cortico-(brain-stem)-spinal projections modulate the spinal excitability in an opposite way. Note that a similar inverted modulation of cortical and spinal activity was shown by Prut & Fetz (1999) by recording in the monkey the activity of cervical interneurons during an instructed delay period and the subsequent movement period. Whereas many premotor and motor cortex cells have been shown to increase their activity during the instructed delay, most of the recorded interneurons showed a suppression of activity during the same period. Although the degree of specificity of such an inhibition is still unclear, these findings suggest that during instructed delay two different mechanisms are working at the spinal level: a subthreshold preparation to move and a superimposed suppression of overt movement. In the case of action observation a highly specific mechanism is working: spinal excitability is modulated in a way opposite to that expected during active execution of the task possibly to prevent the overt replica of the seen actions. Note that the presence of such a peripheral, movement-specific inhibition may favour the cortical processing of observed actions, leaving the cortical motor system to ‘re-act’ the observed actions without the risk of overt movements generation. This ‘motorically silent’ mapping of observed actions on the observer’s motor repertoire might be at the basis of the identification/recognition process of actions performed by other individuals.

Acknowledgements
This work was supported by Italian MURST and Human Frontier Science Program. The authors wish to thank Roger N. Lemon, Eberhard E. Fetz and Maurizio Gentilucci for their helpful comments on the manuscript.

Abbreviations
EMG, electromyography; FDS, flexor digitorum superficialis; MEP, motor-evoked potential; M wave, maximum direct motor response; TMS, transcranial magnetic stimulation.

References


