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Motor Facilitation During Action Observation: A Magnetic Stimulation Study

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SUMMARY AND CONCLUSIONS

1. We stimulated the motor cortex of normal subjects (transcranial magnetic stimulation) while they *1*) observed an experimenter grasping 3D-objects, *2*) looked at the same 3D-objects, *3*) observed an experimenter tracing geometrical figures in the air with his arm, and *4*) detected the dimming of a light. Motor evoked potentials (MEPs) were recorded from hand muscles.

2. We found that MEPs significantly increased during the conditions in which subjects observed movements. The MEP pattern reflected the pattern of muscle activity recorded when the subjects executed the observed actions.

3. We conclude that in humans there is a system matching action observation and execution. This system resembles the one recently described in the monkey.

INTRODUCTION

It is well established that in the monkey there is a hand movement representation in inferior area 6 (Kurata and Tanji 1986; Rizzolatti et al. 1981, 1988; see also Matsumura and Kubota 1979; Muakkassa and Strick 1979). This representation is located near the arcuate sulcus and is largely coextensive with area F5 of Matelli et al. (1985). An important characteristic of F5 is that many of its neurons discharge during goal-directed motor acts such as grasping, manipulating, holding, and tearing (Rizzolatti et al. 1988). In recent experiments, we demonstrated that a particular subset of F5 neurons become active both when the monkey makes goal directed movements and when it *observes* similar movements executed by other individuals, i.e., another monkey (G. Rizzolatti, L. Fadiga, V. Gallisi, L. Fogassi, in preparation) or an experimenter (di Pellegrino et al. 1992). These data appear to indicate that when the monkey observes a motor action, that is present in its natural movement repertoire, this action is automatically, covertly retrieved. We speculated that this mechanism may play a role in understanding the meaning of motor events.

In the present study we addressed the problem of whether an observation/execution matching system, as that found in the monkey, is present also in humans. The assumption underlying the experiment was that, if the observation of a movement activates the premotor cortex also in man, this activation should induce an enhancement of motor evoked potentials (MEPs) elicited by the magnetic stimulation of the motor cortex (see Barker et al. 1985). The anatomic pathways that may mediate this enhancement are the cortico-cortical connections linking premotor and motor areas, and/or the pathways connecting directly (Dum and Strick 1991; He et al. 1993) or indirectly (Keizer and Kuypers 1989) the premotor areas with the spinal cord. Regardless of which pathway could mediate the effect, the results showed a clear enhancement of MEPs during action observation.

METHODS

The experiments were carried out on 12 normal human subjects. All but one of them were naive to the purpose of the experiment; they all gave their informed consent for the experimental procedure. The subjects sat on comfortable armchairs with their elbow flexed at 90° and hands pronated in a totally relaxed position. Their heads were fixed in a modified cephalostat for temporomandibolar radiology.

Left motor cortex was stimulated using transcranial magnetic stimulation (see Edgley et al. 1990; Rothwell et al. 1987). Magnetic stimuli were delivered by a focal ''butterfly-shaped'' coil (Dantec Electronics, DK) with the handle oriented rostrally. The coil was attached to the cephalostat by a Plexiglas bar, that could be moved tangentially on the skull of the subjects by an X-Y-Z moving system. Motor evoked potentials (MEPs) were recorded using Ag-AgCl surface electrodes from the following four muscles: extensor digitorum communis (EDC), flexor digitorum superficialis (FDS), first dorsal interosseus (FDI), and opponens pollicis (OP). EMG sweeps (prestimulus record, 240 ms; poststimulus record, 360 ms) were band-pass filtered (20–2,000 Hz), digitized, and recorded on a computer for a successive off-line analysis. The prestimulus records were used to assess the possible presence of an EMG activity before TMS. Trials in which such an activity was present were extremely rare and randomly distributed across the four experimental conditions (see below). They were discarded from analysis.

Each subject underwent one ''calibration'' and one experimental session. In the calibration session, we orderly stimulated the motor cortex moving the coil in the rostro-caudal and medio-lateral directions until we localized the sites with the lowest excitability threshold for each recorded muscle. On the basis of these data, we selected a point on the skull from which we could elicit low threshold short latency MEPs (Edgley et al. 1990) from all recorded muscles. This point was then stimulated during the experimental session.

There were four different experimental conditions. *1) Grasping observation.* The subject had to observe the experimenter grasping an object. Objects of different size and shape (e.g., spheres, boxes, and commonly used objects) were employed in different trials. *2) Object observation.* The same objects as above were presented to the subject, who had to observe them attentively for about 3 s. *3) Arm movement observation.* The subject had to observe the experimenter who traced in the air a relatively complex geometric shape with his arm extended and the hand relaxed in a prone position. In different trials different shapes were drawn (e.g., squares, crosses, Greek alphabet letters: alpha, omega, etc.). *4) Dimming detection.* The subject had to detect, and verbally signal, as fast as possible, the dimming of a light stimulus (2° diam red filled circle, 20% intensity reduction) appearing on a computer screen. The time between the stimulus presentation and dimming was randomly selected (range 2–4 s).

Subjects were subdivided into two groups of six individuals each. The difference between the two groups was the way in which subjects were induced to pay attention to visual stimuli. In the first group this was achieved by asking the subjects to observe carefully the stimuli and, in some trials, to imitate the last observed action in the case of the two movement observation conditions and to grasp the last observed object in the case of the object observation condition. The trials in which subjects had to execute movements occurred randomly, on average one out of four trials. In the second group, the subjects were also asked to observe carefully the stimuli but, in addition, they were informed that, at the end of the experimental session, they would be presented with some grasping and arm movements as well as objects, and they would have to tell the experimenters which among these stimuli they had seen during the experimental session. They were not asked to perform any movement.

Each subject underwent 32 trials, 8 for each experimental condition, randomly intermixed. In conditions one, two, and three, transcranial magnetic stimulation (TMS) was delivered just before the end of stimulus presentation; in the dimming detection task it was delivered between light presentation and dimming. An interval of at least 15 s elapsed between two successive TMSs. The subjects were instructed to remain completely relaxed throughout the trials. A rest condition was not included in the experimental design, because of the large MEP variability that is observed when subjects are not involved in cognitive or motor activities (see Kiers et al. 1993).

In six subjects, three from each group, the EMG activity was recorded during rest, active grasping, and arm elevation from the same four muscles studied during magnetic stimulation. In each subject, eight trials were recorded for each condition. Data were collected as above and the root mean square (RMS) of the recorded EMGs was calculated off-line. In both grasping and arm elevation RMS was calculated on the EMG activity of the movement period of each trial. For rest condition, RMS was calculated on EMG records (essentially noise) of 500 ms.

RESULTS

Action observation

Four analysis of variance tests (ANOVAs) were performed, one for each recorded muscle: EDC, FDS, FDI, and OP. The main factors were Group (2 levels) and Experimental condition (4 levels). The results showed that Experimental condition only was significant (EDC: $F = 7.12$, df = 3, $P = 0.001$; FDS: $F = 5.89$, df = 3, $P = 0.002$; FDI: $F = 13.16$, df = 3, $P = 0.00001$; OP: $F = 12.34$, df = 3, $P = 0.00002$).

Figure 1 shows the mean values of the MEPs recorded from the muscles in the four experimental conditions. During "grasping observation" (■) the MEP amplitude of the recorded muscles increased with respect to the conditions in which visual stimuli were not related to actions (left and right rising lines bars). During "arm movement observation" (□) the increase was present in all muscles except OP. Duncan multiple pairwise comparisons ($P < 0.01$) performed for each muscle showed that the two movement observation conditions differed significantly from the other two for EDC, FDS, and FDI. For OP the grasping condition only differed significantly from the other three. Figure 2 illustrates the MEPs of one subject recorded during the four experimental conditions.

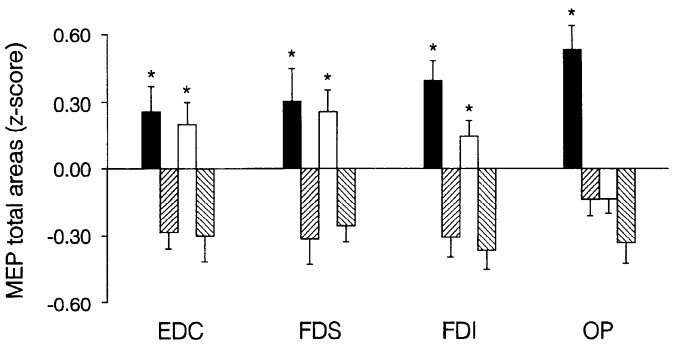

FIG. 1. Mean values of the recorded motor evoked potentials (MEPs) for all subjects in the 4 experimental conditions. Abscissae: recorded muscles. Ordinates: z-score of MEP total areas. The normalization was performed for each muscle in each subject. Grasping observation (■); object observation (▨); arm movement observation (□); dimming detection (▧). ±SE is indicated on each bar. Conditions indicated by asterisks significantly differed from those without asterisks and did not differ one from another. EDC, extensor digitorum communis; FDS, flexor digitorum superficialis; FDI, first dorsal interosseus; OP, opponens pollicis.

Action execution

The data described above and, in particular, the differential behavior of the OP muscle during the two movement observation conditions raise the question of whether the muscles that are facilitated during the observation of a given action are those that are active also during its execution. This should be true for OP, which is active during active grasping, but not during arm elevation. Less obvious is the behavior of FDI, and in part of FDS, that should be involved in the grasping, but, in theory, could play also some hand stabilizing role during arm elevation. To answer these questions, we recorded the EMG activity during rest, object grasping, and arm lifting, from the same muscles that were recorded during TMS. Data from six subjects were collected and averaged. The results are shown in Fig. 3. During grasping all the recorded muscles became significantly more active than during rest. In contrast, during arm elevation there was a significant increase of activity in EDC, FDS, FDI, while OP remained virtually silent.

DISCUSSION

The results of the present experiment demonstrate that the excitability of the motor system increases when a subject observes an action performed by another individual. Furthermore, the pattern of muscle activation evoked by transcranial magnetic stimulation (TMS) during action observation is very similar to the pattern of muscle contraction present during the execution of the same action. These findings indicate that, in humans, there is a neural system matching action observation and execution. A similar system was recently described in the monkey (di Pellegrino et al. 1992).

The possibility that the facilitatory effects on MEP amplitude were due to motor preparation for a possible impending movement or to unspecific factors (arousal or intensive attention) was ruled out by the two experimental conditions in which visual stimuli did not represent action. The mere observation of an object, even if it was the target for a possible movement, did not produce any effect comparable to that occurring during movement observation. Furthermore, the

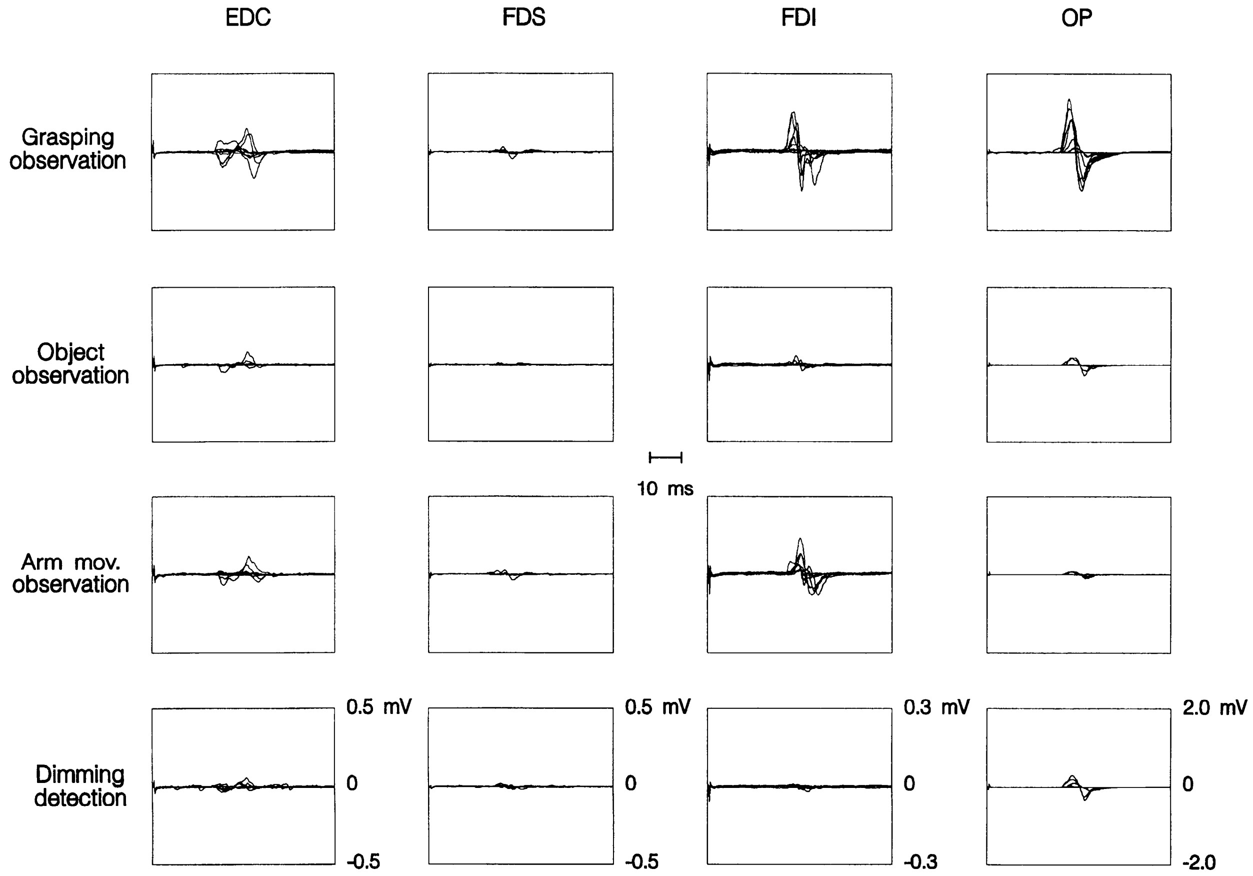

FIG. 2. Effects of observation of hand and arm movements on the magnetic evoked potentials. The MEPs of one subject are presented. Each panel shows all superimposed responses (n = 8) evoked from the indicated muscle in one condition. Traces are aligned with and shown from the stimulus onset.

presence of the facilitatory effect in those subjects who were required to inspect the stimuli, but not to act on them (Group 2) indicates that the facilitatory effect depended on mere observation of the actions and not on a possible ''mental practice'' induced by the instruction to perform occasionally those actions (Group 1). Similarly, attentional effect could be excluded because the highly attention-demanding dimming detection task produced no obvious MEPs change. This last finding is in line with previous data showing that mental tasks requiring attention have no influence on the MEP amplitude of hand muscles (Kiers et al. 1993).

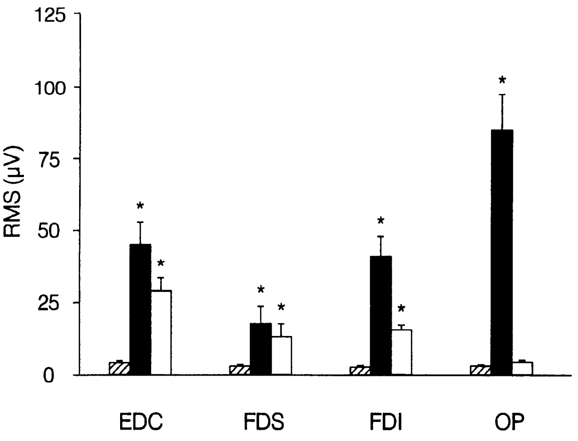

FIG. 3. Mean values of EMG activity recorded during object grasping and arm elevation. The averaged values (RMS) of 6 subjects recorded from four hand muscles during rest (▨), grasping (■) and arm elevation (□) are shown. ±SE is indicated on each bar. Asterisks indicate the conditions that are significantly different from rest (t-test for dependent samples, $P < 0.05$). EDC, extensor digitorum communis; FDS, flexor digitorum superficialis; FDI, first dorsal interosseus; OP, opponens pollicis. For other abbreviations see Fig. 1.

There is evidence that during execution of a motor task TMS can reveal the set of muscles specifically selected for it (Johansson 1993). The present findings show that, in the absence of movement or even of a voluntary movement preparation (see for comparison Gandevia and Rothwell 1987), the observation of an action automatically recruits neurons that would normally be active when the subject executes that action. TMS reveals this automatic facilitation by transforming it into an overt EMG activation. It appears therefore that the motor system, in man as in monkey, is not solely devoted to the production of movements, but it is also involved in their recognition. It is an open question if such a recognition subserves only motor purposes or is also involved in conscious interpretation of actions (see Jeannerod 1994; Liberman and Mattingly 1985).

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