



Corticospinal excitability is specifically modulated by motor imagery: a magnetic stimulation study

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Abstract

Transcranial magnetic stimulation (TMS) was used to investigate whether the excitability of the corticospinal system is selectively affected by motor imagery. To this purpose, we performed two experiments. In the first one we recorded motor evoked potentials from right hand and arm muscles during mental simulation of flexion/extension movements of both distal and proximal joints. In the second experiment we applied magnetic stimulation to the right and the left motor cortex of subjects while they were imagining opening or closing their right or their left hand. Motor evoked potentials (MEPs) were recorded from a hand muscle contralateral to the stimulated cortex.

The results demonstrated that the excitability pattern during motor imagery dynamically mimics that occurring during movement execution. In addition, while magnetic stimulation of the left motor cortex revealed increased corticospinal excitability when subjects imagined ipsilateral as well as contralateral hand movements, the stimulation of the right motor cortex revealed a facilitatory effect induced by imagery of contralateral hand movements only. In conclusion, motor imagery is a high level process, which, however, manifests itself in the activation of those same cortical circuits that are normally involved in movement execution. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Motor system; Transcranial magnetic stimulation (TMS); Motor evoked potentials (MEPs); Motor imagery; Hand movement; Hemispheric asymmetry

1. Introduction

Electrophysiological evidence recently showed that actions are stored in the brain as goal related motor schemes. Single unit recordings performed in the monkey ventral premotor cortex (area F5) demonstrated that neurons in this region selectively discharge during goal-directed hand actions [37]. The specificity of the goal seems to be an essential prerequisite in activating these neurons: the same neurons that discharge during grasping, holding, tearing, manipulating, are silent when the monkey performs actions that involve a similar muscular pattern but with a different goal (i.e. grasping to put away, scratching, grooming, etc.). Many grasping neurons, the most represented class of hand related F5 neurons, are selective for a particular type of prehension (precision grip, finger prehension, whole hand prehension) [37].

All these data indicate that in the ventral premotor cortex a ‘vocabulary of actions’ is stored [37, 38]. The presence of such a ‘vocabulary’ may strongly facilitate the execution of motor commands and endows the brain with a storage of ‘action schemes’ related to the specification of action goals [23].

This vocabulary of actions can be addressed not only during action execution. Recent experiments have shown that many F5 neurons (‘canonical’ neurons) discharge at the mere visual presentation of objects whose shape and size is congruent with the type of grip coded by the same neurons [31, 37]. A second class of F5 grasping neurons, ‘mirror’ neurons, are selectively activated when the monkey observes another individual performing actions similar to those they motorically code [18]. It was proposed that mirror neurons represent an observation/execution matching system, possibly involved in understanding actions made by others. The properties of both canonical and mirror neurons demonstrate that the same pool of motor schemes can be visually addressed either by objects or by action observation.

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The possibility to visually address a similar motor vocabulary in humans was demonstrated by a recent experiment in which the excitability of the corticospinal system was tested by transcranial magnetic stimulation (TMS) while subjects observed a series of goal-related hand actions performed by the experimenter in front of them [16]. During action observation, the motor evoked potentials (MEPs) recorded from subjects' hand muscles significantly increased with respect to different control conditions. In addition, the observed pattern of hand muscle facilitation was congruent with that observed during actual execution of similar actions.

The activation of action vocabulary either during the execution of transitive movements or during observation of objects or of actions performed by others, is triggered by the presence of external stimuli. On the other hand, the evolutionary process has provided the human brain with the possibility to mentally represent 'things' (actions, objects, emotions, etc.) by means of the voluntary process of thought, also in the absence of any external trigger. It is a common experience that we can mentally represent actions simply by thinking about them. This process of mental representation of movements is usually defined as motor imagery. According to Jeannerod [22]: 'Motor imagery would be a part of a broader phenomenon (the motor representation)'. During motor imagery, the subject 'looks' at its own motor repertoire and 'feels' himself to move 'from the inside'.

The idea that motor imagery could share phenomenological aspects with movement execution is supported by several findings: (1) The main vegetative parameters, such as heart rate, blood pressure, and breath frequency significantly increase during mental simulation of movements strictly correlating with the strength of the effort [see 11]; (2) The duration of imagined actions is similar to that of the same actions when actually executed [12]; (3) Many brain imaging studies showed an increase of regional cerebral blood flow (rCBF) in various cortical motor areas and cerebellum during motor imagery tasks [13, 17, 19, 36, 39, 41, 44, 47]. Similar results were recently achieved by magnetoencephalography [20, 45] and movement related potentials [5, 9].

It is not completely clear, however, if these movement-related phenomena are due to unspecific factors such as intention or readiness to move, or if they rather reflect a true internal dynamic simulation of movement. This issue can be addressed by using TMS, a technique that allows one to measure the corticospinal excitability with high sensitivity and, most importantly, with high temporal resolution, thus providing a precise description of the excitation/inhibition pattern present in the corticospinal system at the moment of the stimulation [4, 28, 42]. The reliability of this technique in revealing the gross modulation of corticospinal excitability exerted by movement simulation, cortical plasticity and motor learning was previously shown by several authors [1, 24, 33–35, 48, 49].

In the present paper we will present the results of two TMS experiments in which we investigated the problem of the specificity of action representation and dynamics during motor imagery.

In the first experiment the excitability of arm and hand muscles was assessed by stimulating the left precentral cortex during mental simulation of right forearm extension and flexion and right hand opening and closing. In the second experiment, in addition to the specific effect induced by imagined movements on hand muscles, the different contribution of the two hemispheres to motor imagery of ipsilateral and contralateral hand movements was also investigated.

2. Experiment 1

2.1. Method

2.1.1. Subjects

Six, right handed, human subjects (2 males and 4 females) participated in the experiment. Age ranged from 23 to 35 (mean, 28). All of them, but one (author), were naive as to the purpose of the experiment and gave their informed consent. The experimental procedure was approved by the Parma University Ethical Committee.

2.1.2. Procedure

The experiment was performed in a sound attenuated room, dimly illuminated. Subjects sat on an armchair with their elbow flexed at 90° and their hands half-pronated in a totally relaxed position. The subject's head was fixed in a modified cephalostat for temporomandibular radiology.

Left motor cortex was stimulated by using single pulse TMS (Dantec Electronics, DK). Magnetic stimuli were delivered through a circular coil placed on the skull with the handle positioned in a medio-lateral orientation. The coil handle was attached to the cephalostat and could be moved tangentially on the skull by a three-axes moving system.

The experiment was subdivided into two sessions. In the first session (*proximal arm motor imagery*), subjects were required to imagine flexing and extending their right forearm. In the second session (*distal arm motor imagery*), subjects were asked to imagine opening and closing their right hand by opposing the thumb to the other fingers. Imagined movements were continuously guided by a frequency modulated sound: the frequency increasing phase corresponded to the imagined hand opening or forearm flexion, while the frequency decreasing phase guided the imagined hand closing or forearm extension. In both sessions, as a control, there was a second task devoid of motor content: subjects were asked to generate a *visual image* of an expanding/shrinking light bar, that was previously shown to the subjects on a computer screen. The

expanding/shrinking of the visual bar was accompanied by the same sound as in the motor imagery task. The visual imagery control condition was introduced to assess the degree of non-specific activation (or arousal) of the corticospinal system during imagery.

In both sessions electromyographic recordings (EMGs) were made with Ag–AgCl surface electrodes (diameter 6 mm) glued to the subjects' skin.

In Session 1 (proximal arm motor imagery) EMGs were recorded from right proximal arm muscle Biceps Brachialis (BB, agonist for elbow flexion) and from right intrinsic hand muscle Opponens Pollicis (OP). The OP recordings were performed to test the specificity of motor imagery process: the prediction was that motor imagery of proximal movements should involve proximal muscles only.

In Session 2 (distal arm motor imagery) EMGs were recorded from right intrinsic hand muscle OP (agonist of hand closing). Furthermore, in four subjects, EMG of right Extensor Digitorum Communis (EDC, an antagonist of hand closing and agonist of hand opening), was also monitored. The recorded muscles were selected to test the effect of imagined movement on the excitability of those corticospinal pathways that during real execution participate as agonist/antagonist with respect to hand opening (agonist: EDC, antagonist: OP and FDI) and closing (agonist: OP and FDI, antagonist: EDC).

Before each experimental session, the coil position was selected to obtain reliable MEPs in all recorded muscles.

TMS was randomly delivered 100 to 300 ms from the onset of either phases of the sweeping sound, with an interval of at least 15 s between two successive stimulations. EMG sweeps (pre-stimulus record, 300 ms; post-stimulus record, 300 ms) were band-pass filtered (20–800 Hz), digitized (sample rate 2 KHz), and recorded on a computer for the successive off-line analysis. The pre-stimulus records were used to assess the possible presence of EMG activity before TMS. Trials in which EMG activity was present were very rare and randomly distributed across all experimental conditions. These trials were discarded from analysis.

Each subject underwent eight stimulations for each experimental condition. The order of stimulations was randomly selected and balanced among subjects.

2.2. Results and discussion

2.2.1. Session 1 (proximal arm motor imagery)

Figure 1 shows the individual data recorded from one subject (upper four panels) and mean z -score of BB MEP areas recorded during imagined forearm extension and flexion expressed as difference from the control condition (visual imagery of expanding-shrinking bar). Statistical analysis showed that the two imagined movements differently affected the excitability of BB muscle (t -student test: $t(5) = -3.2$, $P < 0.05$): MEP amplitude was

larger during motor imagery of forearm flexion than during motor imagery of forearm extension. Conversely, as shown in Fig. 2, OP muscle excitability recorded during motor imagery of the same proximal movements was not significantly influenced by the task.

2.2.2. Session 2 (distal arm motor imagery)

OP muscle excitability was significantly influenced during motor imagery of hand movements ($t(5) = -3.2745$, $P < 0.05$, see Fig. 3). MEP amplitude was larger during motor imagery of hand closing than during motor imagery of hand opening. This pattern was congruent to the role of agonist that the OP muscle plays during actual hand closing. The EDC muscle (recorded from four subjects) showed an excitability pattern that, although not statistically significant, was the reversal of that exhibited by OP muscle during the same task (see Fig. 4). Note that during actual movement, EDC muscle is an agonist of hand opening.

These results showed that specific corticospinal channels are selectively influenced by the internal simulation of movement. This experiment demonstrated both effector-specific and movement-specific effects of motor imagery.

The effector-specific effect is shown by the influence exerted by hand and forearm imagined movements on hand and arm muscles, respectively. Furthermore, the OP muscle recorded during proximal arm imagery did not show a task dependent modulation of MEP amplitude.

The movement-specific effect is clearly shown by the fact that imagery of a movement only affects the MEPs of muscles that are involved during actual execution of that movement. Recorded MEPs are larger when the imagined movement involves the muscle as agonist with respect to when the imagined movement involves the same muscle as antagonist.

3. Experiment 2

3.1. Method

3.1.1. Subjects

Six, right handed, human subjects (4 males and 2 females), different from those of Experiment 1, participated in the experiment. Age ranged from 24 to 31 (mean, 26). All subjects were naive as to the purpose of the experiment and gave their informed consent to the experimental procedure that was approved by the University of Parma Ethical Committee.

3.1.2. Procedure

The general experimental set up was the same as in Experiment 1.

In two different experimental sessions, left and right motor cortex were stimulated using TMS. Magnetic stim-

Visual imagery

Motor imagery

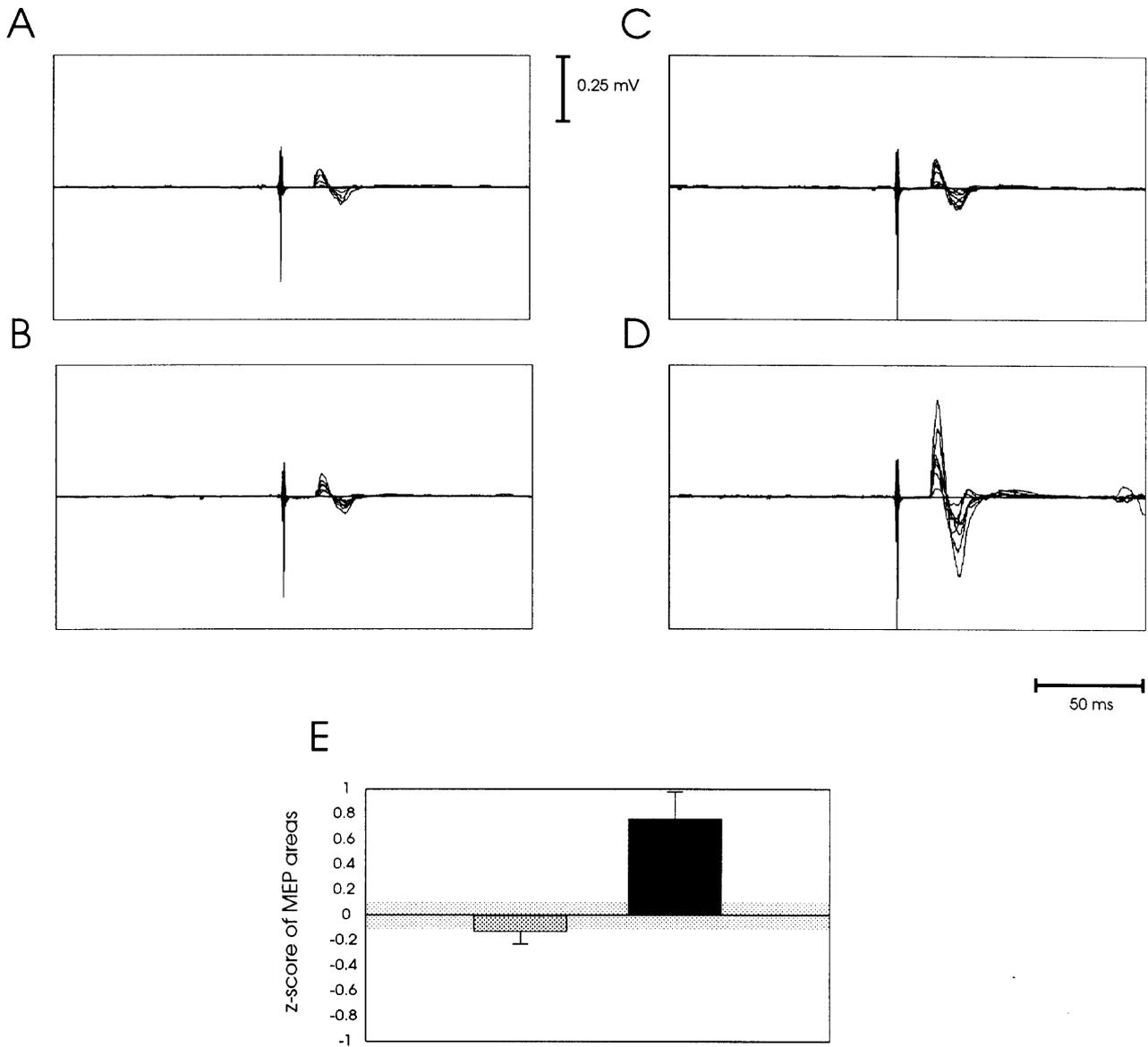


Fig. 1. Effects of motor imagery of forearm extension and flexion on motor evoked potentials (MEPs) of Biceps Brachialis muscle. In A, B, C, D the MEPs of one subject are presented. A, B: visual imagery of expanding and shrinking bar, respectively. C, D: motor imagery of forearm extension and flexion, respectively. Each panel shows all superimposed responses ($n = 8$) evoked from the muscle in one condition. Traces are aligned with the magnetic stimulus onset (magnetic stimulus artifact is visible at the center of recordings). E, Mean values (\pm S.E.) of MEPs for all subjects in the two experimental conditions. Grey bar, imagined forearm extension; black bar, imagined forearm flexion. Ordinates: z-score of MEP total areas. Data are represented as difference from the control condition, whose standard error is shown by the grey strip across the horizontal axis (mean values of control condition: -0.17 ± 0.12).

uli were delivered by a focal 'butterfly-shaped' coil (Stimulator MX 5500 A; EsaOte Biomedica, Italy) keeping the handle in a medio-lateral orientation. The coil was attached by means of a spherical joint to a plastic helmet worn by the subjects. This arrangement allowed a good contact between the coil surface and the subjects'

head with a high flexibility in coil positioning. In order to improve EMG selectivity, MEPs from OP muscle were recorded using epoxydic coated tungsten wire electrodes inserted in the subjects' hand muscle (distance between the wires was about 10 mm) contralateral to the stimulated hemisphere. These electrodes gave very good sel-

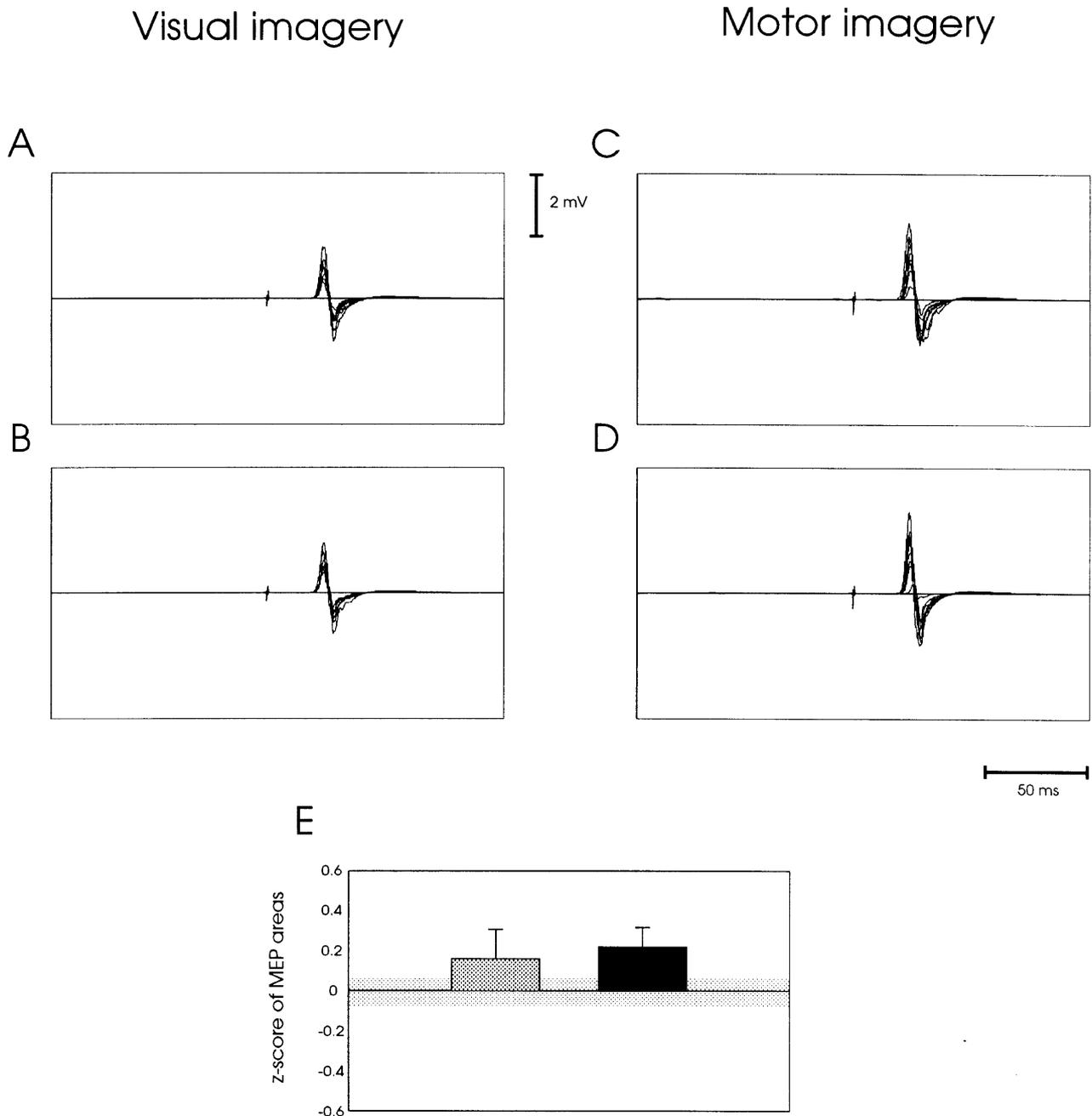


Fig. 2. Effects of motor imagery of forearm extension and flexion on motor evoked potentials (MEPs) of Opponens Pollicis muscle. In A, B, C, D the MEPs of one subject are presented. A, B: visual imagery of expanding and shrinking bar, respectively. C, D: motor imagery of forearm extension and flexion, respectively. E, Mean values (\pm S.E.) of MEPs for all subjects in the two experimental conditions. Grey bar, imagined forearm extension; black bar, imagined forearm flexion. Ordinates: z-score of MEP total areas. Data are represented as difference from the control condition, whose standard error is shown by the grey strip across the horizontal axis (mean values of control condition: -0.09 ± 0.14). For other conventions see Fig. 1.

activity in muscle recording and, after insertion, were completely neglected by the subjects.

Each subject underwent one mapping and two experimental sessions. During the mapping session, the motor cortex of both hemispheres was orderly stimulated by moving the coil along the rostro-caudal and medio-lateral directions. The site with the lowest excitability threshold

for the OP contralateral to the stimulated hemisphere was selected for the experimental stimulation.

Subjects were instructed to imagine themselves opening or closing their right or their left hand (motor imagery task). A computer generated sound (duration 1 s) indicated the onset and the end of the imagined movement. As a control, subjects were asked to generate the visual

Visual imagery

Motor imagery

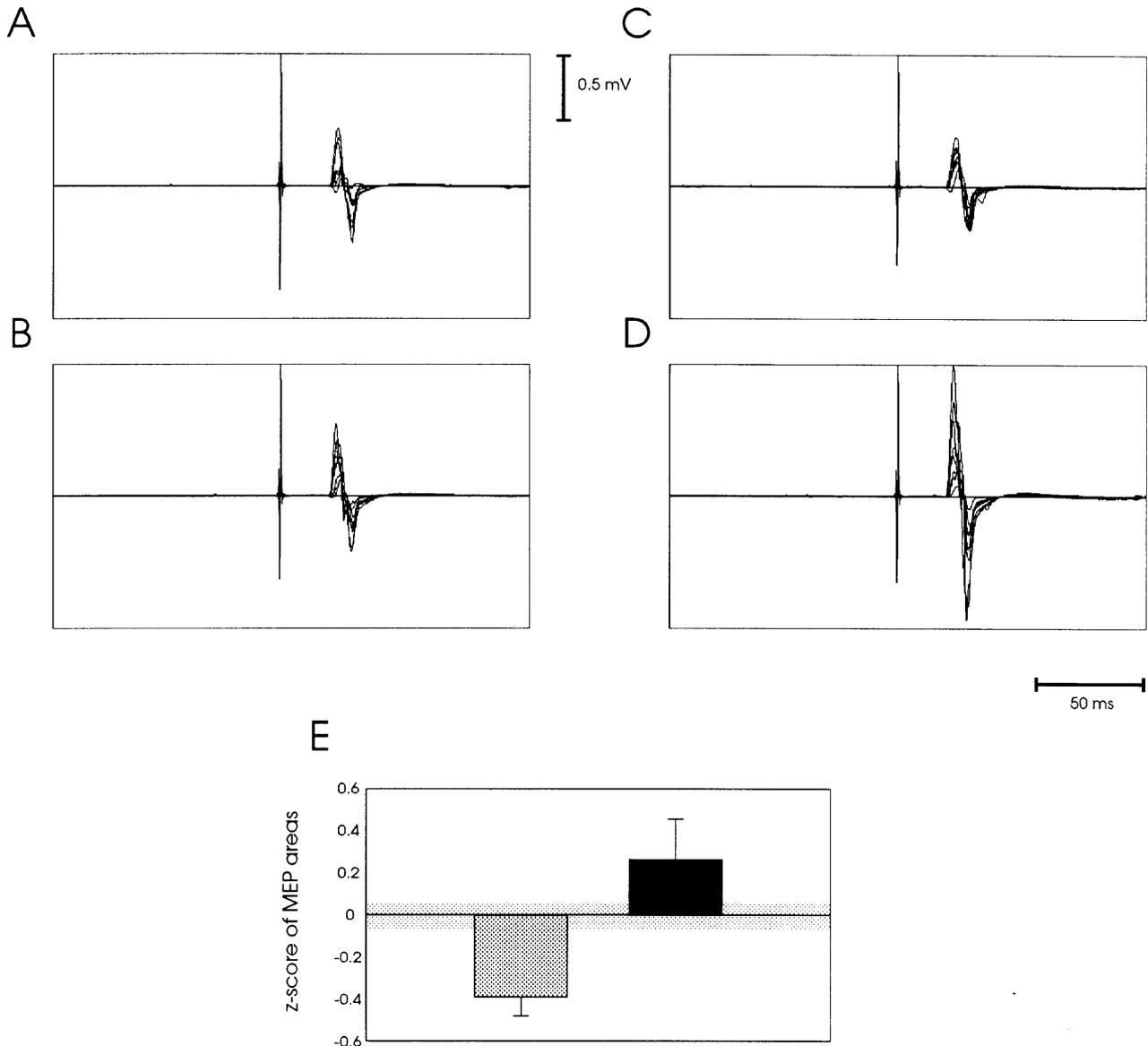


Fig. 3. Effects of motor imagery of hand opening and closing on motor evoked potentials (MEPs) of Opponens Pollicis muscle. In A, B, C, D the MEPs of one subject are presented. A, B: visual imagery of expanding and shrinking bar, respectively. C, D: motor imagery of hand opening and closing, respectively. E, Mean values (\pm S.E.) of MEPs for all subjects in the two experimental conditions. Grey bar, imagined hand opening; black bar, imagined hand closing. Ordinates: z-score of MEP total areas. Data are represented as difference from the control condition, whose standard error is shown by the grey strip across the horizontal axis (mean values of control condition: 0.03 ± 0.12). For other conventions see Fig. 1.

imagery of a previously seen cartoon showing a schematic man going down a schematic mountain (visual imagery task). This task was guided by the same sound that was used in the motor imagery task. Five different experimental conditions were run for each stimulated hemisphere: (1) Motor imagery of the contralateral hand opening; (2) Motor imagery of the contralateral hand

closing; (3) Motor imagery of the ipsilateral hand opening; (4) Motor imagery of the ipsilateral hand closing and (5) Visual imagery. TMS was randomly delivered 200 to 600 ms from the sound onset, with an interval of at least 15 s between two successive stimulations. EMGs were acquired and recorded as in Experiment 1. Data were normalized as in Experiment 1.

Visual imagery

Motor imagery

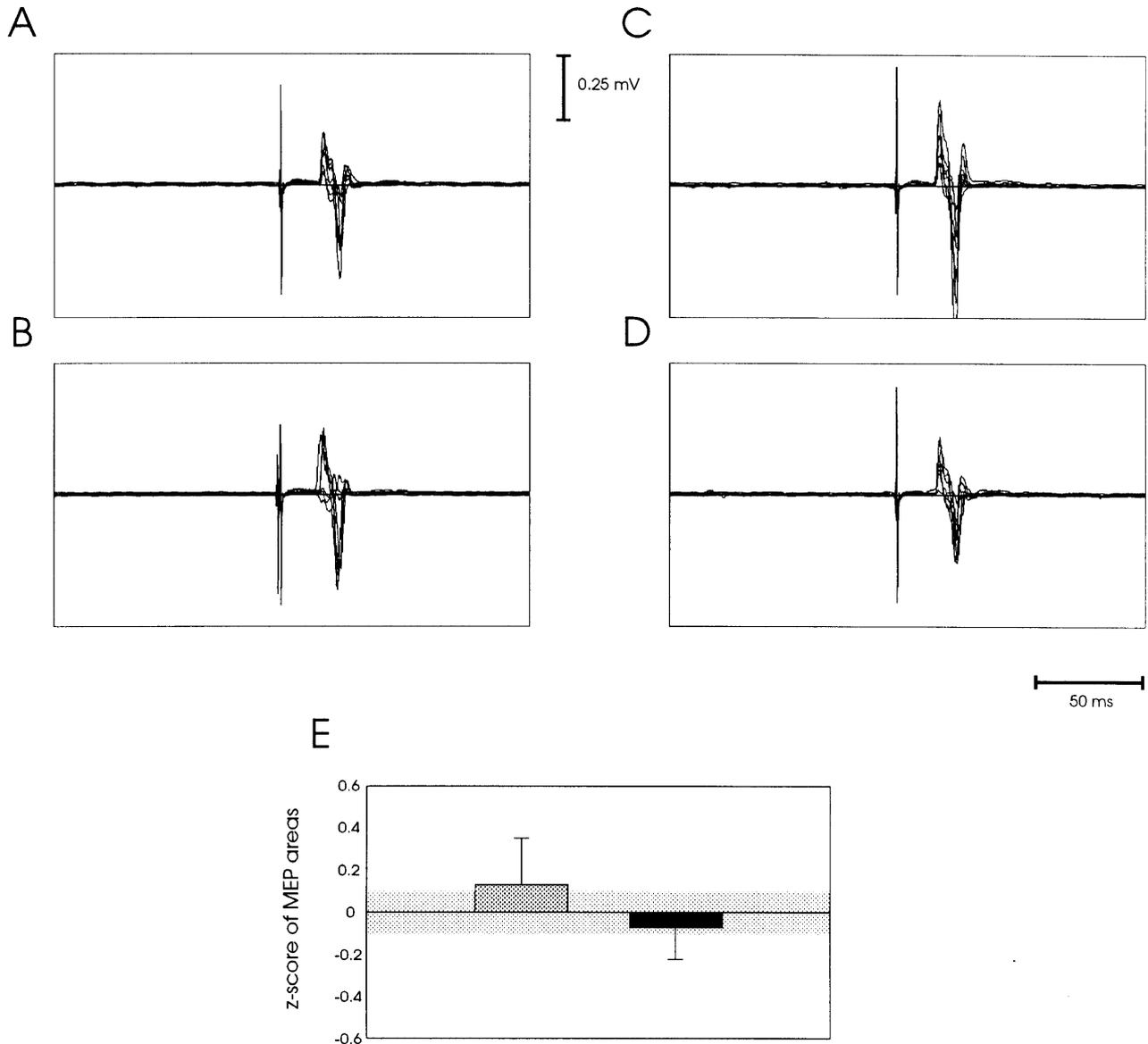


Fig. 4. Effects of motor imagery of hand opening and closing on motor evoked potentials (MEPs) of Extensor Digitorum Communis muscle. In A, B, C, D the MEPs of one subject are presented. A, B: visual imagery of expanding and shrinking bar, respectively. C, D: motor imagery of hand opening and closing, respectively. E, Mean values (\pm S.E.) of MEPs for four subjects in the two experimental conditions. Grey bar, imagined hand opening; black bar, imagined hand closing. Ordinates: z-score of MEP total areas. Data are represented as difference from the control condition, whose standard error is shown by the grey strip across the horizontal axis (mean values of control condition: -0.01 ± 0.12). For other conventions see Fig. 1.

Each subject underwent 20 stimulations for each experimental condition, subdivided into blocks of 10 trials. The presence of learning effects between blocks of the same experimental condition was also tested (see below). The order of experimental condition presentations was balanced among subjects.

3.2. Results and discussion

Figure 5 shows the MEPs of one representative subject in all the experimental conditions. Inspection of the figure demonstrates that during stimulation of the *left* hemisphere, MEP amplitude increased during motor imagery

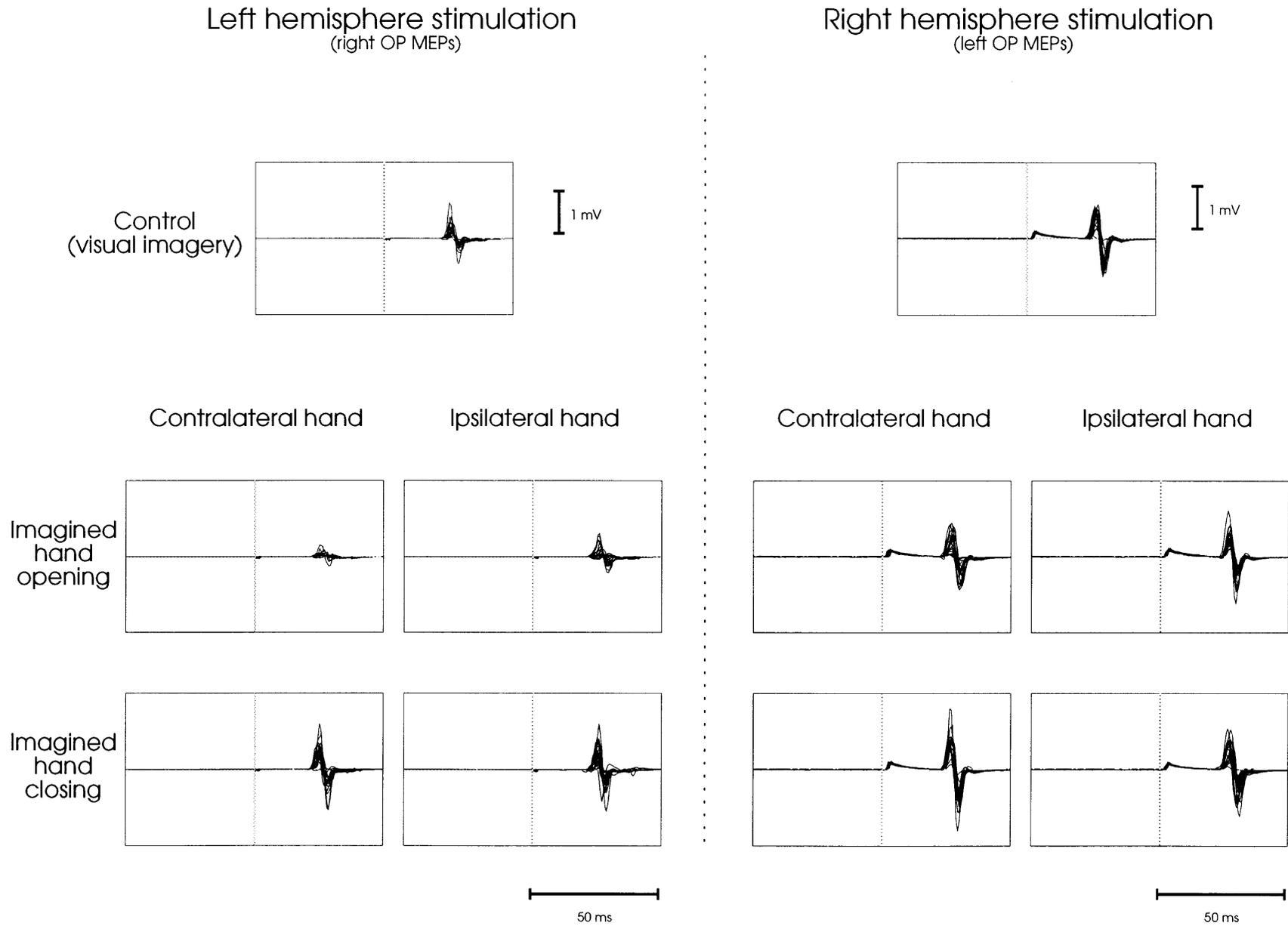


Fig. 5. Effects of motor imagery of hand movements on motor evoked potentials (MEPs) of Opponens pollicis muscle. The MEPs of one subject are presented. Each panel shows all superimposed responses ($n = 20$) evoked from the muscle in one condition. Traces are aligned with the magnetic stimulus onset (grey line across traces).

of contralateral and ipsilateral hand closing with respect to the visual imagery task, whereas they decreased during motor imagery of contralateral and ipsilateral hand opening. During stimulation of the *right* hemisphere, MEP amplitude increased during imagined hand closing, and decreased during imagined hand opening of the contralateral hand, only. Averaged MEP total areas from all subjects are shown in Fig. 6.

Two analyses of variance (ANOVAs) were performed on normalized data, one for the right and one for the left OP. The considered factors were: Hand (ipsilateral, contralateral), Imagined Movement (hand opening, hand closing) and Experimental Block (first, second).

Following *left* hemisphere stimulation (right OP), only the factor Imagined Movement was significant ($F(1,5) = 21.5$, $P < 0.01$). MEP amplitude was larger during motor imagery of hand closing than during motor imagery of hand opening (Fig. 6). Newman-Keuls post hoc analysis performed on the interaction Imagined Movement \times Hand ($F(1,5) = 4.5$, $P = 0.08$) demonstrated that, during imagery of hand closing, MEP amplitude of the contralateral hand was significantly larger than that of the ipsilateral hand ($P < 0.05$). No difference was found between the two opening conditions. The difference between MEP amplitude of imagined hand opening and closing was significant for both the contralateral ($P < 0.01$) and the ipsilateral hand ($P < 0.05$).

Following *right* hemisphere stimulation (left OP), the factor Hand ($F(1,5) = 13.5$, $P < 0.05$) and the two-way interaction Hand \times Imagined movement ($F(1,5) = 26.4$, $P < 0.01$) were significant. A subsequent Newman-Keuls post-hoc analysis showed that MEPs recorded during motor imagery of contralateral hand closing were significantly larger than those recorded during motor imagery of the opening of the same hand ($P < 0.01$). No differences were observed between imagined closing and imagined opening of the ipsilateral (right) hand.

In both ANOVAs, the factor Experimental Block was not significant suggesting the absence of learning effects.

The present results show, in addition to the movement-specific effect already shown in Experiment 1, a different involvement of the left and the right hemisphere during motor imagery. The left hemisphere is involved during the imagination of movements of both the contralateral and the ipsilateral hand, whereas the right hemisphere is involved only during motor imagery of the contralateral hand.

4. General discussion

The present data, according to previous observations [1, 7, 24, 48, 49], demonstrate that motor imagery influences the corticospinal excitability. Furthermore, experiments 1 and 2 demonstrate that this influence is specifically related to the effector involved in motor imagery and to the type of imagined movement.

In the case of proximal movements, the BB muscle acts as an agonist during forearm flexion and as an antagonist during forearm extension. Motor imagery of forearm flexion, but not motor imagery of forearm extension, enhances BB MEPs. In the case of distal movements, the OP muscle acts as an agonist during hand closing and as an antagonist during hand opening. Motor imagery of hand closing, but not hand opening, caused an enhancement in MEPs recorded from the OP muscle. The opposite tendency was observed in the EDC muscle, which acts in an opposite fashion to the OP muscle during the execution of opening-closing hand movements.

In addition, Experiment 2 showed a clear pattern of lateralization; the left hemisphere plays a dominant role in motor imagery. MEPs in both the contralateral right hand and the ipsilateral left hand were facilitated by TMS over the left hemisphere. By contrast, TMS over the right hemisphere only facilitated MEPs recorded from the contralateral left hand. A left hemisphere predominance during motor imagery was also shown by Beisteiner et al. [5] in a study in which DC brain potentials were recorded when subjects either imagined or executed a sequence of hand movements. DC potentials were larger over the left hemisphere both during imagination and execution of hand movements. The modulation of potentials in central recordings (C3, C4) appeared to be greater on the left side than on the right side.

The modification of MEPs induced by TMS is similar during both executed and imagined movements (OP muscle is active during actual hand closing, BB muscle during forearm flexion, etc.). These results are in agreement with recent TMS experiments performed in humans [28] and monkeys [3] that have clearly shown that cortical excitability (revealed by MEPs recorded from several hand/arm muscles) appears to be modulated according to the different phases of reaching-grasping movements. Furthermore, a lateralization pattern, similar to that observed in the present experiment, was reported by Kim et al. [25] in a fMRI study in which they instructed subjects to perform right and left finger movements. They found that the left motor cortex became active not only during contralateral but also during ipsilateral movements, whereas the right motor cortex was activated by contralateral movements, only. Accordingly, Chen et al. [8], by using repetitive TMS of left and right motor cortex during execution of hand movements, showed that the stimulation of the left motor cortex interfered with the execution of contralateral and ipsilateral hand movements, whereas the stimulation of the right motor cortex affected contralateral hand movements, only. Taken together, these data are in accord with the idea of a dominant role of the left hemisphere in motor planning and motor control. In the same direction is the observations that, very frequently, ideomotor apraxia is seen in patients with parietal lesions of the left hemisphere. This pathology is an important disturbance of motor representations

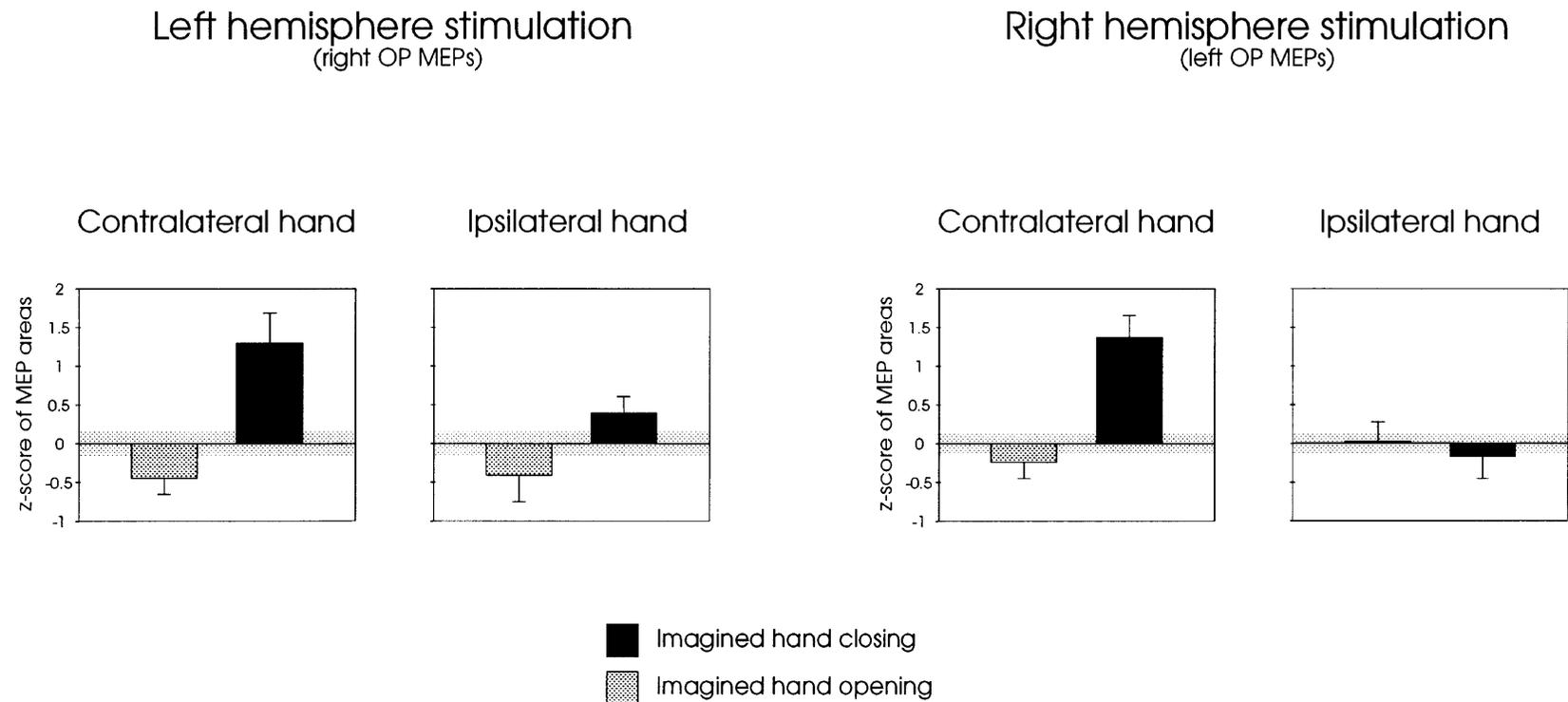


Fig. 6. Mean values (\pm S.E.) of the recorded motor evoked potentials (MEPs) for all subjects in the four experimental conditions. Abscissae: imagined movement. Ordinates: z-score of MEP total areas. The normalization was performed for each muscle in each subject. Data are represented as difference from the control condition, whose standard error is shown by the grey bar on the horizontal axis (mean values of control condition: left hemisphere, -0.17 ± 0.16 ; right hemisphere, -0.2 ± 0.14).

that, while leaving almost intact the capability to act on objects, strongly affects the voluntary retrieval of actions. Among symptoms of ideomotor apraxia are the impairment of the capability to correctly reproduce observed gestures [14, 21, 29], to correctly pantomime object related actions and to execute motor attention demanding tasks [43]. It is important to note that the ipsilateral left hand is affected by ideomotor apraxia in the absence of any clear weakness.

The results shown in the present paper are in agreement with the idea that mental simulation of movements involves the same neural substrate that is addressed during action execution and during observation of actions performed by other individuals [16].

Single neuron recordings performed in monkeys clearly showed that a relevant portion of premotor neurons that become active during execution of hand actions, are also activated by the mere observation of similar actions performed by other individuals [18] (see Introduction). Our data suggest that in humans a similar observation/execution matching system may also constitute the cortical substrate for ‘thinking about movements’.

Further support for this interpretation comes from a study by Sirigu et al. [46] on brain damaged patients. These authors reported the case of a frontal patient who was markedly slower in both execution and imagery of pointing movements even if in both tasks, according to Fitt’s law, there was a good correlation between execution time (in the motor imagery task, the conclusion of the movement was verbally declared by subjects) and task difficulty. According to the ‘vocabulary’ hypothesis (see Introduction), the impairment of action execution due to the lesion is mirrored by an analogue impairment in action imagery.

What is the role of motor imagery? There is evidence to suggest that mental retrieval of motor representation may play an important role in refining motor abilities and in solving non-motor tasks.

Firstly, it seems plausible that, at least in its preliminary phase, motor preparation might benefit from an unconscious (implicit) motor imagery, which allows one to test the plausibility of a *given action* in a *given context* by analysing the different possibilities of interaction with the environment. Secondly, it is well known that athletes benefit in their training of mental simulation of sport exercises [see 2, 6, 27, 30] and that motor imagery is usefully utilized in microsurgery training [15]. Thirdly, some recent experimental data have demonstrated the involvement of the motor system in solving tasks apparently devoid of motor content. In a PET experiment Parsons et al. [32] instructed subjects to judge whether pictures of hands, rotated by various angles, depicted the left or right hand. Motor related areas were clearly activated during task performance. The authors suggested that in order to answer the question, subjects had to mentally rotate their own hand, and were therefore

performing an implicit motor imagery task. A further example of an implicit use of motor imagery was given by de’ Sperati and Stucchi [10] in a study in which subjects were required to recognize the direction of motion of a tool. They showed that reaction times were faster when the stimulus was oriented for the subjects’ dominant hands.

In conclusion, motor imagery should be considered a particular case of a general principle of economy in neural processing. Mental motor representations do not require a dedicated cognitive system; they rely, instead, on the same neural circuits that are used for the generation of actions. Other mental representations, such as visual imagery, depend on the same neural circuit that is activated during visual stimulation [26, 40]. Thus, mental representations, traditionally ascribed to the cognitive domain, appear to be strictly linked and, possibly, intrinsic to the ‘acting’ and ‘perceiving’ brain.

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