

Enhancement of force after action observation Behavioural and neurophysiological studies[☆]

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Abstract

We tested here the hypothesis that observing others' actions can facilitate basic aspects of motor performance, such as force production, even if subjects are not required to immediately reproduce the observed actions and if they are not aware that observation can form the basis for procedural training. To this end, we compared in healthy volunteers the effects of repeated actual execution (MOV) or observation (OBS) of a simple intransitive movement (abduction of the right index and middle fingers). In a first experiment, we found that both actual and observational training significantly increased the finger abduction force of both hands. In the MOV group, force increases over pre-training values were significantly higher in the trained than in the untrained hand (50% versus 33%), whereas they were similar for the two hands in the OBS group (32% versus 30%). No force change was found in the control, untrained group. In a second experiment, we found that both training conditions significantly increased the isometric force exerted during right index finger abduction, whereas no post-training change in isometric force was found during abduction of the right little finger. Actual performance, imagination and, to a lower extent, observation of fingers movement enhanced the excitability of the corticospinal system targeting the first dorsal interosseus muscle, as tested by transcranial magnetic stimulation; pre- and post-training effects were of similar magnitude.

These results show a powerful, specific role of action observation in motor training, likely exerted through premotor areas, which may prove useful in physiological and rehabilitative conditions.

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1. Introduction

How do we acquire new motor skills, or improve existing ones? In many instances, watching actions performed by experienced subjects has a pivotal role, e.g. while practicing a new sport discipline. Investigating the principles and neural mechanisms underlying learning by action observation is an important issue for researchers of different disciplines (Byrne & Russon, 1998; Heyes, 2001; Meltzoff & Prinz, 2002).

Current neuropsychological theories postulate that perceived events and planned actions share a common representational domain, and specifically that perception of an action should activate inner representations of similar actions (Jeannerod, 2001; Prinz, 1997; Rizzolatti, Fogassi, & Gallese, 2001). They mainly base their claims on neurophysiological studies in non-human primates, providing insights into the neural mechanisms that could subserve action representation in response to visual input. The so-called mirror neuron system (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti & Fadiga, 1998), originally discovered in monkey ventral premotor cortex (area F5), is one of the best candidates for such a matching between action observation and action execution. A large set of evidence has been provided that a visuomotor resonant system, sharing some similarities with that described at the single cell level in monkeys,

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does exist in the human cortex (Blakemore & Decety, 2001; Buccino et al., 2001; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Rizzolatti et al., 1996; see also Rizzolatti & Craighero, 2004 for a recent review). Neuroimaging studies in humans suggest a partial overlap between the cortical areas involved in action execution, imagination and observation (Decety & Grezes, 1999; Grezes & Decety, 2001; Lui et al., 2007). Recent studies point to an involvement of the human mirror system both in the imitation of simple motor acts (Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003; Iacoboni et al., 1999; Nishitani & Hari, 2000) and of new complex finger postures (Buccino et al., 2004; Tanaka & Inui, 2002).

Learning by action observation can however occur at different levels of complexity and over different time courses (Boschker & Bakker, 2002; Byrne & Russon, 1998; Meltzoff & Prinz, 2002; Vinter & Perruchet, 2002); imitation is usually a volitional process in adults, yet simple imitation can occur without conscious awareness (Tessari, Rumiati, & Haggard, 2002). It is still unclear whether, and by which mechanisms, repeated observation can implicitly enhance performance of pre-learned movements, even if subjects are not required to immediately reproduce the observed actions and are not aware that observation can form the basis for procedural training. This is an important point, that would make observational training quite different from motor imagery training, that requires an explicit intention to mentally represent a given action, then being a voluntary process (Ranganathan, Siemionow, Liu, Sahgal, & Yue, 2004; Yue & Cole, 1992). This difference may assume particular relevance for rehabilitation purposes: the finding that observational training could involve the motor system at its lower levels may support new rehabilitation approaches where patients are simply requested to pay attention to visually presented movements. To address this issue, we compared the behavioural effects of repeated observation or actual execution of a simple intransitive finger movement (abduction of the right index and middle fingers against an elastic resistance). We purposely chose a movement that can be made without *ex novo* learning, yet is seldom performed in isolation in everyday life and it is therefore amenable to improvement by exercise.

As a first step towards understanding the neural mechanisms that could underlie observation-related changes in motor performance, we have also compared using transcranial magnetic stimulation (TMS) the changes in corticospinal excitability induced by actual execution, kinaesthetic motor imagery or observation of the same movement, both pre- and post-training.

2. Methods

The studies were carried out in 82 healthy right-handed volunteers (38 males, 44 females, aged 19–33 years, mean 21.9), after informed consent and approval of the local Committee on Ethics. All of them were students of the University of Udine, had normal or corrected-to-normal visual acuity and were free from neurological or muscular disorders or any condition precluding TMS such as pacemakers, intracranial metallic material and, in the case of women, pregnancy. They were unaware that the purpose of the study was to detect potential effects of repeated observation on motor performance. Volunteers were paid for their participation.

2.1. Behavioural experiments

Two behavioural experiments were carried out. In the first experiment, we studied changes in the maximal voluntary isotonic force exerted by abduction of the right index and middle fingers, following actual training or repeated passive observation. In the second experiment, we investigated whether the effects of actual or observed finger abduction could be detected also in a maximal isometric force abduction test, and whether they were also present in fingers not directly involved in the trained task.

2.1.1. Experiment 1

Twenty-seven volunteers (11 males, 16 females, aged 21–33, mean 22.8 years) took part in the first experiment. Subjects were randomly assigned to one out of three groups ($n=9$ per group): Movement (MOV: four males, five females, mean age 22.3 years), Observation (OBS: three males, six females, mean age 23 years) and Control (CONT: four males, five females, mean age 23.1 years).

Subjects in the MOV group were trained in a simple finger abduction task consisting in pull away the second from the third finger of the right hand against the resistance of a rubber band, that was positioned immediately proximal to the second interphalangeal joint of the index finger. Six daily training sessions were carried out in pairs (one subject of the MOV served as stimulus for one subject of the OBS groups), over two consecutive weeks. During each training session, subjects of the MOV group executed 25 abduction movements of the right index and middle fingers, each lasting about 3 s: they were instructed to exert their maximal abduction force in each trial and to not communicate their feelings to subjects of the OBS group. Movements were separated from each other by 25 s of rest. Two trial series (for a total of 25 trials), separated by a 3 min interval, were performed daily. During each training session, volunteers of the OBS group sat in front of subjects of the MOV group: they were instructed to keep their arms relaxed and to carefully observe finger movements, in order to catch all visual aspects of the scene. Volunteers of the OBS group were explicitly told that they had not to reproduce the observed action throughout the training sessions; they could not hear the instruction given before training to the subjects of the MOV group. As a test of their attention to the tasks, subjects of the OBS group were asked to report the number of observed trials, immediately after each series. During training, subjects of both MOV and OBS groups wore a similar rubber band. No subject of the OBS group showed overt fingers or hand movements during training or reported themselves imagining performing the observed movement. However, two volunteers spontaneously reported to “feel an increased tone in my arm” (see Berger, Carli, Hammersla, Karshmer, & Sanchez, 1979). Although we did not record electromyographic activity (EMG) during the experiments, we did so in some pilot trials without observing any significant difference in EMG background activity among the various conditions. Subjects in the CONT group did not undergo any kind of motor training.

In each volunteer of the three groups, we measured the maximal abduction isotonic force of the index and middle fingers on three separate sessions: before the beginning of training (Baseline – BAS), after the first training session (Post-training, EARLY) and after 6 days of training (Post-training, LATE). Subjects of the different groups were tested separately, so volunteers of the OBS group could not see testing of subjects of the MOV group. During the testing sessions, we measured the maximal abduction isotonic force in the horizontal plane, using a double load cell device (one for each finger) built in our laboratory (Fig. 1).

The averaged force exerted by the two fingers was taken as the dependent variable. Five measurements were taken for finger abduction movements of the right and left hand, with an inter-trial interval of approximately 30 s. The order by which right and left fingers were tested varied randomly across subjects. Values were recorded trial-by-trial and analyzed off-line. Subjects were not aware of the developed force in each trial. No specific visual stimulus was presented during the testing procedures.

2.1.2. Experiment 2

Twenty-eight (16 males, 12 females) healthy right-handed volunteers (mean age 21.0 years, range 20–33), different from the ones who took part in the first experiment, were studied. They were randomly assigned to the MOV ($n=9$; seven males, two females, mean age 21 years), OBS ($n=9$; four males, five

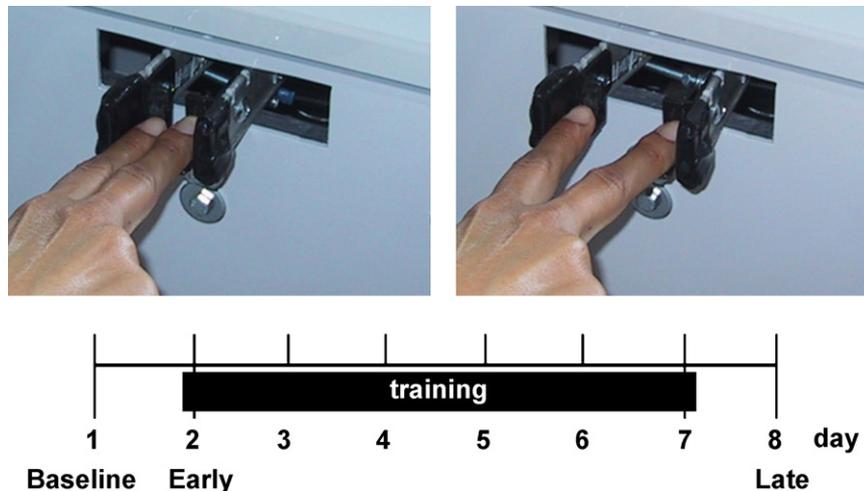


Fig. 1. (Top) Index and middle finger position during testing of the abduction isotonic force. (Bottom) Experimental design. Post-training (Late) testing occurred after six daily training sessions. In Experiment 1, a further test (Early) took place after the first training session.

females, mean age 22.1 years) and CONT ($n=10$; five males, five females, mean age 20.1 years) groups.

The training protocol was identical to the one described for Experiment 1. Two testing sessions (Baseline – BAS and LATE) were performed at an 8-days interval (namely, the day before and the day after the end of training for subjects of the MOV and OBS groups, respectively).

To measure muscle isometric contraction force a custom-built force transducer, composed of a wooden structure unity provided with a load cell and a digital processor, was used. All subjects were seated comfortably on a chair. To standardize the starting position for the force measurements and to minimize the involvement of other muscle groups, subjects' forearms had joints blocked by a plastic splint that allowed only the 2nd and 5th fingers abduction in a way similar to that described by Ranganathan et al. (2004). The splint was in turn fixed to a rigid support by means of wrist and arm restraints. Abduction force measurements were carried out with forearms relaxed in a prone position. Subjects were required to execute maximal isometric contractions during each trial; each movement was repeated four times, with a minimum interval of at least 25 s. As in Experiment 1, subjects of the different groups were tested separately, so volunteers of the OBS group could not see testing of subjects of the MOV group.

2.1.3. Statistical analysis

All data are presented as mean (\pm S.E.M.). Statistical comparisons on behavioural data were performed by analysis of variance (ANOVA), with Group as the between-subjects factor. The within-subjects factors were Hand (right or left) and Session (BAS, EARLY and LATE) in Experiment 1, and Hand, Finger (index or little) and Session (BAS and LATE) in Experiment 2. Post hoc comparisons were done by Student's *t*-test if appropriate. A *P*-value less than 0.05 was assumed as the threshold for significance.

2.2. TMS experiments

In a third experiment, we compared using transcranial magnetic stimulation (TMS) the effects of actual, imagined or observed finger movements on corticospinal excitability, both before and after a 6-days training period.

2.2.1. Experiment 3

We tested 27 volunteers (11 males and 16 females, age range 20–30 years), different from the ones who took part in Experiments 1 and 2. Volunteers were randomly assigned to one out of three experimental groups ($n=9$ per group): Movement (MOV: five males, four females, mean age 21.7 years), Motor Imagery (IMA: three males, six females, mean age 21 years) and Observation (OBS: three males, six females, mean age 23.1 years).

The experiment consisted of a pre-training TMS session, a 6 days training period, and a post-training TMS session. Subjects in the MOV and OBS groups

were trained under the same protocol as in Experiments 1 and 2. Volunteers in the IMA group underwent six daily sessions, during which they were trained one at a time in a kinaesthetic imagination task (so-called "first-person" motor imagery; Jeannerod & Frak, 1999), involving the same movement as in the MOV and OBS groups. Two trial series (for a total of 25 3-s trials), separated by a 3 min interval, were performed daily. Volunteers were instructed to keep their upper limb muscles as relaxed as possible during the task.

The TMS sessions took place in a sound-attenuated room, dimly illuminated. Participants were seated on a motorized dental armchair with both elbows flexed and their hands supinated in a relaxed position. Participants' head was laying on a headrest and the backrest was regulated at about 45° to maintain a comfortable and stable head position.

The left motor cortex was stimulated by using a Magstim Rapid Magnetic Stimulator (Magstim Co., UK). Biphasic magnetic stimuli were delivered through an eight-shaped coil placed tangentially to the skull, with the handle pointing upwards in a medio-lateral orientation. During the first mapping session, magnetic stimuli were applied on predetermined positions of a one-centimeter grid drawn on a latex swimming cap worn by participants. The coordinate origin was located at the Cz reference point determined according to the International 10–20 EEG system. Motor-evoked potentials (MEPs) were recorded from the right hand first dorsal interosseus muscle (FDI) by using 6 mm Ag–AgCl surface electrodes (Kendall GmbH, Germany) glued to the participants' skin according to a tendon-belly bipolar disposition. The first step in the TMS session consisted of localizing the site on the left hemiscalp from which the highest responses could be evoked in the contralateral FDI, with the stimulator set at 70% of its maximal output. Once the optimal spot was localized (so called "hot-spot"), the site was marked with a red dot to ensure consistent coil positioning; the coil was kept in a stable position by means of an articulated arm. After detecting the hot-spot, the intensity of stimulation was gradually reduced and the relaxed FDI motor threshold (presence of detectable MEPs in 5 out of 10 successive stimuli) was established. The stimulus intensity was adjusted at 110% of the FDI motor threshold and maintained at this level during the experiment. Each experimental session lasted about 45 min. In the rare event of coil displacement, for instance to accommodate participants (e.g. after coughing), the experimenter used the marks drawn on the cap to reposition the coil over the same previous site.

During each TMS session, volunteers of each group underwent a mapping procedure at rest and during their assigned motor task (MOV, IMA or OBS, respectively). The FDI muscle activity was constantly monitored on a high gain oscilloscope to ensure that full relaxation was maintained both during rest, IMA and OBS tasks. Three magnetic stimuli were applied on each of nine points arranged like a 3 cm \times 3 cm square (the FDI hot-spot and eight surrounding points spaced 1 cm apart): thus, we obtained 27 MEPs for each condition during each experimental session. In volunteers of the MOV and OBS groups, the TMS pulse was delivered at the time of maximal displacement of the second and third finger. All volunteers put on a rubber band around the right index

and middle fingers throughout the experiments. The MEPs evoked from 100 ms before to 100 ms after TMS pulses were band-pass filtered (50–1000 Hz), digitized (2000 Hz) and stored on a computer. The peak-to-peak amplitude of FDI MEPs were then calculated off-line, and averaged for each condition and each experimental session.

2.2.2. Statistical analysis

Statistical comparisons on MEPs amplitudes were performed by analysis of variance (ANOVA), with Group as the between-subjects and Session (pre- and post-training) and Task (Rest or Motor Task) as the within-subjects factors. Post hoc comparisons were done by Student's *t*-test if appropriate. A *P*-value less than 0.05 was assumed as the threshold for significance.

3. Results

3.1. Experiment 1

Mean (\pm S.E.M.) values of fingers abduction force at Baseline were 425 ± 36 g for the right hand and 462 ± 34 g for the left hand. ANOVA performed on data from the three groups (MOV, OBS, and CONT) showed a significant effect of Session ($F_{2,48} = 40.55$, $P < 0.0001$). Post-training (LATE) values were significantly higher than baseline (BAS) ones (simple contrasts: $F_{1,24} = 44.46$, $P < 0.0001$), whereas values recorded immediately after the first training session (Early training: EARLY) were not ($F_{1,24} = 1.00$, ns). The Session \times Group interaction was also significant ($F_{4,48} = 7.61$, $P < 0.0001$), whereas no significant Hand effect was found ($F_{1,24} = 0.73$, ns). Considering both hands, BAS values were not significantly different among groups ($F_{2,24} = 0.63$, ns), nor were changes in EARLY values ($F_{2,24} = 1.95$, ns). By contrast, we found significantly higher LATE changes in the OBS and MOV groups, in comparison with control subjects who underwent no training ($F_{2,24} = 8.69$, $P < 0.001$; OBS versus CONT, $P < 0.01$, MOV versus CONT, $P < 0.001$).

In both MOV and OBS groups, the force exerted during abduction of the right fingers was increased in the LATE test, in comparison to the BAS and EARLY ones (MOV group: $F_{2,16} = 37.13$, $P < 0.001$; OBS group: $F_{2,16} = 18.74$, $P < 0.001$). Mean LATE increases over baseline were approximately 50% in the MOV and 32% in the OBS group. No change in motor performance over time was found in the Control group ($F_{2,16} = 1.38$, ns) (Fig. 2).

A significant effect of actual or observed training was also found on the force exerted during the same kind of movement by the left (untrained) index and middle fingers. LATE values in the MOV ($F_{2,16} = 8.32$, $P < 0.005$) and OBS ($F_{2,16} = 8.50$, $P < 0.005$) groups, but not in CONT subjects ($F_{2,16} = 0.79$, ns) were higher than the BAS and EARLY values (Fig. 2). LATE force improvement was higher for the trained hand than in the untrained hand in the MOV group (50% versus 33%: $t = 2.80$, $P < 0.05$), whereas it was of similar extent for the two hands in the OBS group (32% versus 30%: $t = 0.25$, ns).

3.2. Experiment 2

ANOVA showed differences in the isometric force exerted by abduction of the index and little finger, as expected

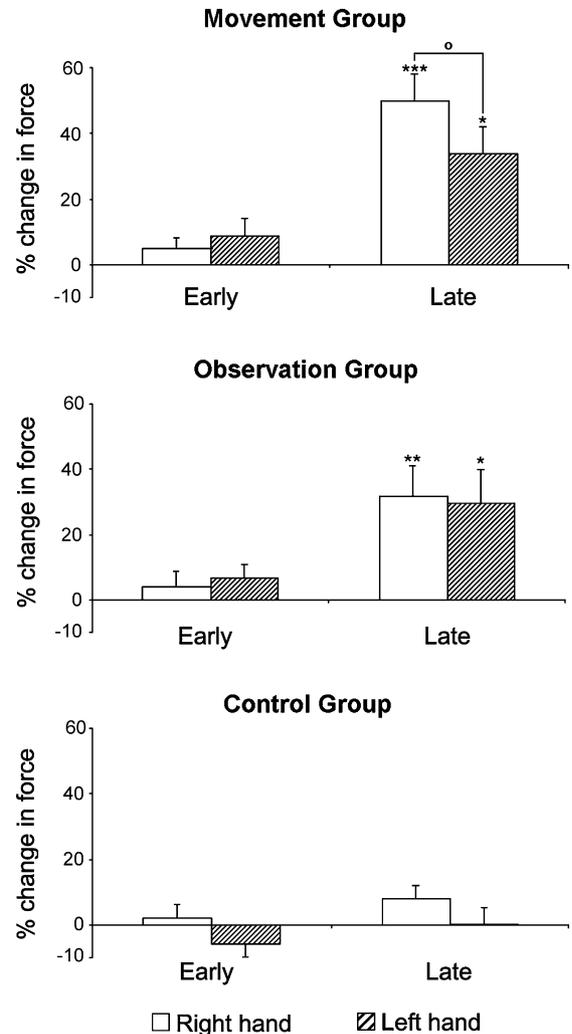


Fig. 2. Mean percentage changes relative to baseline values of peak isotonic force exerted during abduction of the index and middle fingers, after the first training session (Early) or after 6 days (Late) of training involving the right hand. In subjects who underwent actual (Movement group) or implicit (Observation group) training, force developed during maximal voluntary abduction of either right hand or left hand fingers increased at the end of training. In the Control group, re-testing at comparable intervals without intervening training did not yield any significant change in force. *, **, and *** significantly different from baseline (pre-training) and Early values, $P < 0.05$, < 0.01 and < 0.001 , respectively; ° values from the trained hand higher than those from the untrained hand, $P < 0.05$.

($F_{1,25} = 122.7$, $P < 0.0001$). The Session \times Finger \times Group ($F_{2,25} = 4.9$, $P < 0.02$) and Session \times Finger \times Hand ($F_{1,25} = 7.66$, $P < 0.01$) interactions were also significant.

Post hoc analyses showed that the force exerted during right index finger abduction differed according to the group and session (Session: $F_{1,25} = 12.07$, $P < 0.005$; Session \times Group: $F_{2,25} = 5.21$, $P < 0.05$). Indeed, LATE values were about 15% higher than BAS ones in both the MOV ($t = 2.72$, $P < 0.05$) and OBS ($t = 3.46$, $P < 0.01$) groups, whereas no change over time was found in controls ($t = 0.72$, ns) (Fig. 3). No post-training change in performance was found for the force exerted by the right little finger or the left index and little fingers.

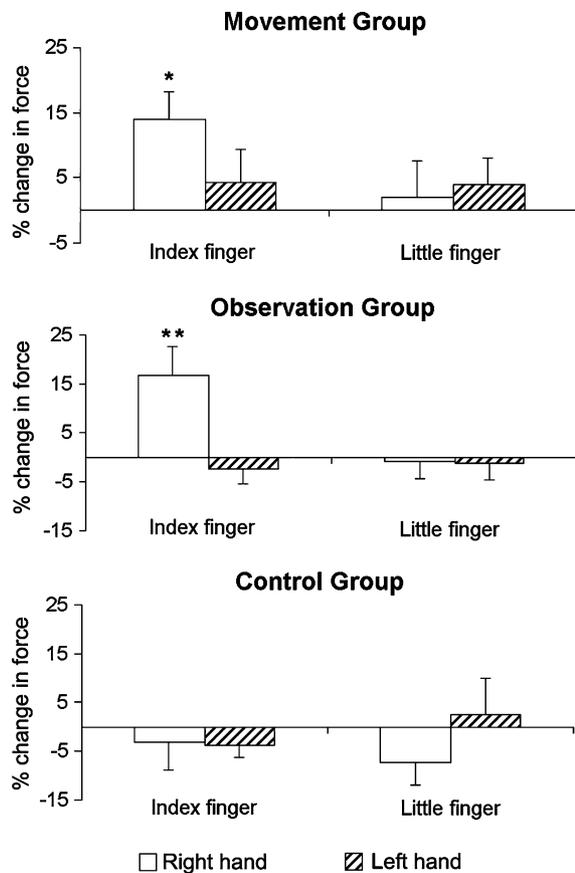


Fig. 3. Mean percentage changes relative to baseline values of peak isometric force exerted during abduction of the index or little fingers, after 6 days of actual (movement) or implicit (observation) training involving the right index and middle fingers. *' and '**', significantly different from baseline (pre-training) values, $P < 0.05$ and < 0.01 , respectively.

3.3. Experiment 3

ANOVA on MEPs from the three groups (MOV, IMA, and OBS) showed a significant effect of Group ($F_{2,24} = 15.04$, $P < 0.0001$) and Task ($F_{1,24} = 81.81$, $P < 0.0001$), and a significant Task \times Group interaction ($F_{2,24} = 23.42$, $P < 0.001$). No significant effect of Session (pre- or post-training: $F_{1,24} = 0.32$, ns) nor a significant Session \times Group, or Session \times Group \times Task interaction was found. Values recorded at Rest were not significantly different among groups ($F_{2,24} = 0.58$, ns). By contrast, during the motor tasks a significant difference in MEPs amplitudes was found ($F_{2,24} = 19.59$, $P < 0.0001$), values recorded during actual movement and motor imagery being significantly higher than those recorded during motor observation ($P < 0.001$ and < 0.05 , respectively).

Analysis on MEPS from each group showed that MEPs increased during all three motor tasks with respect to rest (MOV group: $F_{1,8} = 44.64$, $P < 0.0001$; IMA group: $F_{1,8} = 47.74$, $P < 0.0001$; OBS group: $F_{1,8} = 5.73$, $P < 0.05$); no significant difference was found in the post-training versus pre-training session, either at rest or during task execution (MOV group: Time: $F_{1,8} = 0.17$, ns; Time \times Task: $F_{1,8} = 0.23$, ns; IMA group: Time: $F_{1,8} = 0.001$, ns; Time \times Task: $F_{1,8} = 0.23$, ns; OBS group: Time: $F_{1,8} = 0.20$, ns; Time \times Task: $F_{1,8} = 0.60$, ns). During both

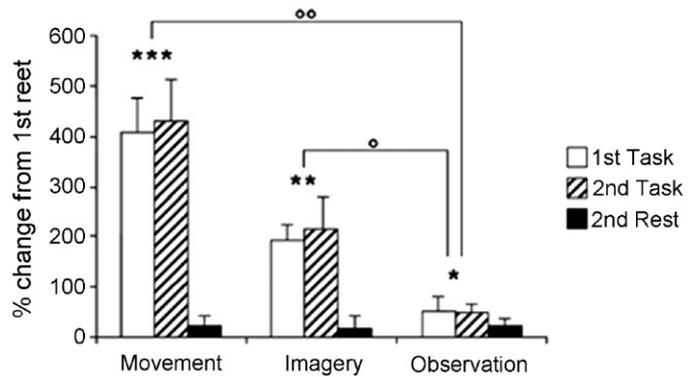


Fig. 4. TMS experiments. Mean percentage increases over baseline values of right FDI MEPs amplitudes during actual, imagined or observed abduction of the right index and middle fingers. 1st and 2nd task: values obtained during the pre-training or post-training session, respectively. *', '**' and '***' significantly different from baseline (1st rest) values, $P < 0.05$, < 0.01 and < 0.001 , respectively; ° significantly higher than the Observation group, $P < 0.05$. No significant MEP amplitude change was found during the post-training vs. pre-training sessions.

sessions, percentage MEPs increases over rest during action observation (+51 and +48%, respectively) were significantly lower than those during motor imagery (+194 and +216%) and during actual motor performance (+408 and +430%) (t -tests: $P < 0.05$ for all comparisons) (Fig. 4).

4. Discussion

The implicit training effect of action observation confirms and extends those of previous studies, suggesting that overt motor practice is not strictly necessary for implicit motor learning (Vinter & Perruchet, 2002). Maximum force production has rarely been used as an indicator of motor performance (but see Yue & Cole, 1992 and Ranganathan et al., 2004); rather, most previous studies investigated learning of motor sequences (e.g. Bird, Osman, Saggerson, & Heyes, 2005; Boschker & Bakker, 2002; Mattar & Gribble, 2005; Osman, Bird, & Heyes, 2005). Our findings are consistent with those of previous studies, showing that motor performance may be facilitated even with observation of simple movements (Brass, Bekkering, & Prinz, 2001; Stefan et al., 2005). Interestingly, the time courses of force improvement were similar for actual and observational training, being evident in our study at the end of the training protocol but not immediately after the first training session. Although our results suggest an improvement in motor performance which is congruent with the observed movements, additional studies involving repeated observation of irrelevant motion patterns are needed to further assess the specificity of the effect.

Because post-training improvements of isotonic force were present for both hands, they are likely attributable mainly to changes in central motor circuits, allowing a more efficient recruitment of spinal motor units. Interestingly, strictly unilateral effects were shown in the isometric force task, both after actual and observational training. It should be noted that only the isotonic task effectively mimics the trained movement. It is conceivable that, under this condition, behavioural improvement is mainly the result of the refinement of the activity of

premotor circuits involved in finger motor coordination (see below), which control the effectors of either hand. In the isometric task, which implies a different strategy of motoneuronal recruitment, force improvement can be tentatively attributed to a memory trace more restricted to the primary motor cortex (M1; see Stefan et al., 2005). We are aware of the speculative nature of these interpretations. Indeed, it may be argued that no significant changes in motor potentials were evoked by TMS between pre- and post-training trials. This lack of corticospinal modifications could be explained, however, by the fact that subjects were performing an ‘overlearned’ movement, which is considered not to alter the excitability of M1 motor maps (Muellbacher, Ziemann, Boroojerdi, Cohen, & Hallett, 2001). Further experiments, differentiating between simple and complex movements (as well as intransitive and transitive – goal-directed – ones) are required to better elucidate this point.

There is increasing evidence that action observation induces behavioural or physiological changes indicative of interference with human motor systems. It has been proposed that observing others’ action can act as a priming stimulus for retrieving a movement already present in the individual’s own repertoire (Byrne & Russon, 1998), thus affecting motor performance. Indeed, observing ideomotor-compatible versus incompatible finger movements or still pictures yield a substantial advantage in reaction times, even in simple response tasks (Brass et al., 2001; Craighero, Bello, Fadiga, & Rizzolatti, 2002). Furthermore, observing another human (but not a robotic arm) making incongruent movements interferes with executed arm movements, thus demonstrating that the simultaneous activation of conflicting neural networks underlying movement observation and execution has a measurable cost to motor control (Kilner, Paulignan, & Blakemore, 2003).

It has to be underlined that, as previously found for motor imagery (Decety, Jeannerod, Germain, & Pastene, 1993), the physiological effects of action observation are not only restricted to the somatic motor system, but also involve vegetative changes. For instance, watching human actors performing effortful tasks increases ventilation rate, e.g. during observation of a weight lifting task (Mulder, de Vries, & Zijlstra, 2005; Paccalin & Jeannerod, 2000) or of a rowing race (Calabrese, Messonnier, Bijaoui, Eberhard, & Benchetrit, 2004). During observation of locomotion, the increases in breathing rate are related to the actor’s running speed, suggesting the activation of central control mechanisms linked to action performance (Paccalin & Jeannerod, 2000).

One possible explanation for the post-training force improvements in the OBS group is that subjects could have spontaneously engaged kinaesthetic motor imagery during the training period. Indeed, imagery training is known to improve performance in different kinds of motor tasks (Annett, 1994; Pascual-Leone et al., 1995; Ranganathan et al., 2004; Yue & Cole, 1992; Zijdewind, Toering, & Bessem, 2003). This explanation seems unlikely, however. On the one hand, motor imagery (an active process) and passive observations are clearly distinct processes on subjective experience, and our volunteers did not report overlap of the two. Moreover, our TMS data show that observation-related changes in corticospinal excitability were,

both in pre- and post-training TMS sessions, much lower than those triggered by motor imagery. Were repeated observation automatically associated with motor imagery, a post-training increase in corticospinal excitability would have been conceivably found during motor observation.

Our TMS data are in line with previous studies showing that observing intransitive hand actions increases the excitability of the motor cortex, although to a lower extent than actual execution (Clark, Tremblay, & Ste-Marie, 2003; Fadiga et al., 1995; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002; Patuzzo, Fiaschi, & Manganotti, 2003; Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005; see for a review Fadiga, Craighero, & Olivier, 2005). Moreover, the present TMS results provide a direct comparison between the neural correlates of actual movement, imagery and observation of the same motor task, which can rarely be found in the literature (Grafton, Arbib, Fadiga, & Rizzolatti, 1996). In a previous TMS study, Clark et al. (2003) found a non-significant trend towards greater increases in corticospinal excitability during observation in order to imitate and imagery (both were considered as active conditions) than during passive observation. The interpretation of their data is difficult, however, because different actions were involved in the passive (a pantomime of scissor-like movements) and active (OK sign) conditions. Meta-analyses of neuroimaging studies in humans led to the suggestion that the neural circuitry involved in action execution overlaps extensively with that activated when actions are imaged or observed (see Decety & Grezes, 1999; Grezes & Decety, 2001). Recent fMRI studies from our group, comparing the brain correlates of motor imagery and observation of complex intransitive hand movements, confirmed that both tasks recruit partially overlapping networks in the lateral premotor cortex; however, significantly higher activity was found during imagery than during observation in several cortical areas, including the supplementary motor area, portions of the inferior frontal gyrus and of the precentral gyrus (Lui et al., 2007). Thus, both fMRI and TMS data support quantitative differences in the activity of cortical motor systems during explicit (motor imagery) and implicit (observation) recruitment of inner motor representations (Jeannerod, 2001).

We found no *net* changes in average corticospinal excitability following actual, imaged or observed training, in comparison with the pre-training data. Our TMS results are thus at variance with those of other groups, showing changes in M1 output maps due to actual or imagined motor training (Pascual-Leone et al., 1995, 1999) or repeated action observation (Stefan et al., 2005). Although negative results must always be interpreted cautiously, one possible explanation for these apparent discrepancies lies in the different kind of motor task (a simple two-finger, pre-learned movement) adopted in our study. Data by Muellbacher et al. (2001) seem to confirm this interpretation.

The identification of brain circuits underlying performance improvements during implicit observational training awaits therefore further investigation. As mentioned before, the bilateral effects found in isotonic maximal abduction force strongly suggest a modulation of the activity of motor/premotor circuits. Brain imaging studies have shown observation-related activity in cortical regions, such as the rostral inferior parietal lobule and

the lower precentral gyrus/posterior inferior frontal gyrus, which are considered to be the core of the putative human mirror system, sharing some similarities with that described at the single cell level in monkeys (Blakemore & Decety, 2001; Buccino et al., 2001; Rizzolatti & Craighero, 2004; Rizzolatti et al., 1996). The human mirror system can be further activated during immediate imitation of simple motor acts (Heiser et al., 2003; Iacoboni et al., 1999; Nishitani & Hari, 2000) and can therefore be tentatively involved in long-term observational training. Interestingly, activation in the lateral premotor cortex is significantly higher when subjects observe manual grasping actions performed by a human actor than during observation of actions performed by a robot model (Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004). These results indicate that the human mirror system is biologically tuned, and strengthen the importance of observing real movements during training (see also Perani et al., 2001).

In conclusion, we show that implicit observational training leads to improvements in the performance of movements already present in the subjects' own repertoire, which are not evident after a brief period of action observation. This suggests that repeated visually evoked motor representations can induce plastic changes in cortical/subcortical circuits controlling motor output in humans, likely by acting at the premotor cortex level. Exploiting this mechanism can prove to be of great value for sport training and rehabilitation purposes.

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References

- Annett, J. (1994). The learning of motor skills: Sports science and ergonomics perspectives. *Ergonomics*, *37*, 5–16.
- Berger, S. M., Carli, L. L., Hammersla, K. S., Karshmer, J. F., & Sanchez, M. E. (1979). Motoric and symbolic mediation in observational learning. *Journal of Personality and Social Psychology*, *37*, 735–746.
- Bird, G., Osman, M., Saggerson, A., & Heyes, C. (2005). Sequence learning by action, observation and action observation. *British Journal of Psychology*, *96*, 371–388.
- Blakemore, S. J., & Decety, J. (2001). From the perception of action to the understanding of intention. *Nature Reviews Neuroscience*, *2*, 561–567.
- Boschker, M. S., & Bakker, F. C. (2002). Inexperienced sport climbers might receive and utilize new opportunities for action by merely observing a model. *Perceptual and Motor Skills*, *95*, 3–9.
- Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica*, *106*, 3–22.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, *13*, 400–404.
- Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J., et al. (2004). Neural circuits underlying imitation learning of hand actions: An event-related fMRI study. *Neuron*, *42*, 323–334.
- Byrne, B. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *Behavioural & Brain Sciences*, *21*, 667–721.
- Calabrese, P., Messonnier, L., Bijaoui, E., Eberhard, A., & Benchetrit, G. (2004). Cardioventilatory changes induced by mentally imaged rowing. *European Journal of Applied Physiology*, *91*, 160–166.
- Clark, S., Tremblay, F., & Ste-Marie, D. (2003). Differential modulation of corticospinal excitability during observation, mental imagery and imitation of hand actions. *Neuropsychologia*, *42*, 105–112.
- Craighero, L., Bello, A., Fadiga, L., & Rizzolatti, G. (2002). Hand action preparation influences the responses to hand pictures. *Neuropsychologia*, *40*, 492–502.
- Decety, J., & Grezes, J. (1999). Neural mechanisms subserving the perception of human actions. *Trends in Cognitive Sciences*, *3*, 172–178.
- Decety, J., Jeannerod, M., Germain, M., & Pastene, J. (1993). Vegetative response during imagined movement is proportional to mental effort. *Behavioural Brain Research*, *51*, 1–5.
- Fadiga, L., Craighero, L., & Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. *Current Opinions in Neurobiology*, *15*, 213–218.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, *73*, 2608–2611.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.
- Grafton, S. T., Arbib, M. A., Fadiga, L., & Rizzolatti, G. (1996). Localization of grasp representations in humans by PET. 2. Observation compared with imagination. *Experimental Brain Research*, *112*, 103–111.
- Grezes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, *12*, 1–19.
- Heiser, M., Iacoboni, M., Maeda, F., Marcus, J., & Mazziotta, J. C. (2003). The essential role of Broca's area in imitation. *European Journal of Neuroscience*, *17*, 1123–1128.
- Heyes, C. (2001). Causes and consequences of imitation. *Trends in Cognitive Sciences*, *5*, 263–271.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*, 2526–2528.
- Jeannerod, M. (2001). Neural simulation of action. A unifying mechanism for motor cognition. *Neuroimage*, *14*, 103–109.
- Jeannerod, M., & Frak, V. (1999). Mental imaging of motor activity in humans. *Current Opinion in Neurobiology*, *9*, 735–739.
- Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed biological movement on action. *Current Biology*, *13*, 522–525.
- Lui, F., Buccino, G., Duzzi, D., Benuzzi, F., Crisi, G., Baraldi, P., & et al. (2007). Neural substrates for observing and imagining non object-directed actions. *Social Neuroscience*, doi:10.1080/17470910701458551.
- Maeda, F., Kleiner-Fisman, G., & Pascual-Leone, A. (2002). Motor facilitation while observing hand actions: Specificity of the effect and role of observer's orientation. *Journal of Neurophysiology*, *87*, 1329–1335.
- Mattar, A. A., & Gribble, P. (2005). Motor learning by observing. *Neuron*, *46*, 153–160.
- Meltzoff, A. N., & Prinz, W. (2002). *The imitative mind. Development, evolution and brain bases*. Cambridge, UK: Cambridge University Press.
- Muellbacher, W., Ziemann, U., Boroojerdi, B., Cohen, L., & Hallett, M. (2001). Role of the human motor cortex in rapid motor learning. *Experimental Brain Research*, *136*, 431–438.
- Mulder, T., de Vries, S., & Zijlstra, S. (2005). Observation, imagination and execution of an effortful movement: More evidence for a central explanation of motor imagery. *Experimental Brain Research*, *163*, 344–351.
- Nishitani, N., & Hari, R. (2000). Temporal dynamics of cortical representation for action. In *Proceedings National Academy of Sciences USA*, *97* (pp. 913–918).
- Osman, M., Bird, G., & Heyes, C. (2005). Action observation supports effector-dependent learning of finger movement sequences. *Experimental Brain Research*, *165*, 19–27.
- Paccalin, C., & Jeannerod, M. (2000). Changes in breathing during observation of effortful actions. *Brain Research*, *862*, 194–200.
- Pascual-Leone, A., Dang, N., Cohen, L. G., Brasil-Neto, J. P., Cammarota, A., & Hallett, M. (1995). Modulation of muscle responses evoked by transcranial

- magnetic stimulation during the acquisition of new fine motor skills. *Journal of Neurophysiology*, 74, 1037–1045.
- Pascual-Leone, A., Tarazona, F., Keenan, J., Tormos, J. M., Hamilton, R., & Catala, M. D. (1999). Transcranial magnetic stimulation and neuroplasticity. *Neuropsychologia*, 37, 207–217.
- Patuzzo, S., Fiaschi, A., & Manganotti, P. (2003). Modulation of motor cortex excitability in the left hemisphere during action observation: A single- and paired-pulse transcranial magnetic stimulation study of self- and non-self-action observation. *Neuropsychologia*, 41, 1272–1278.
- Perani, D., Fazio, F., Borghese, N. A., Tettamanti, M., Ferrari, S., Decety, J., et al. (2001). Different brain correlates for watching real and virtual hand actions. *Neuroimage*, 14, 749–758.
- Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, 9, 129–154.
- Ranganathan, V. K., Siemionow, V., Liu, J. Z., Sahgal, V., & Yue, G. H. (2004). From mental power to muscle power-gaining strength by using the mind. *Neuropsychologia*, 42, 944–956.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192.
- Rizzolatti, G., & Fadiga, L. (1998). Grasping objects and grasping action meanings: The dual role of monkey rostroventral premotor cortex (area F5). *Novartis Foundation Symposia*, 218, 81–95.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of actions. *Nature Reviews Neuroscience*, 2, 661–670.
- Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D., et al. (1996). Localization of grasp representations in humans by PET: 1. Observation versus execution. *Experimental Brain Research*, 111, 246–252.
- Romani, M., Cesari, P., Urgesi, C., Facchini, S., & Aglioti, S. M. (2005). Motor facilitation of the human cortico-spinal system during observation of biomechanically impossible movements. *Neuroimage*, 26, 755–763.
- Stefan, K., Cohen, L. G., Duque, J., Mazzocchio, R., Celnik, P., Sawaki, L., et al. (2005). Formation of a motor memory by action observation. *Journal of Neuroscience*, 25, 9339–9346.
- Tai, Y. F., Scherfler, C., Brooks, D. J., Sawamoto, N., & Castiello, U. (2004). The human premotor cortex is ‘mirror’ only for biological actions. *Current Biology*, 14, 117–120.
- Tanaka, S., & Inui, T. (2002). Cortical involvement for action imitation of arm/hand postures versus finger configurations: An fMRI study. *Neuroreport*, 13, 1599–1602.
- Tessari, A., Rumiati, M. I., & Haggard, P. (2002). Imitation without awareness. *Neuroreport*, 13, 2531–2535.
- Vinter, A., & Perruchet, P. (2002). Implicit motor learning through observational training in adult and children. *Memory and Cognition*, 30, 256–261.
- Yue, G., & Cole, K. J. (1992). Strength increases from the motor program: Comparison of training with maximal voluntary and imagined muscle contractions. *Journal of Neurophysiology*, 67, 1114–1123.
- Zijdewind, I., Toering, S. T., & Bessem, B. (2003). Effects of imagery motor training on torque production of ankle plantar flexor muscles. *Muscle Nerve*, 28, 168–173.