COGNITIVE NEUROSCIENCE

Force requirements of observed object lifting are encoded by the observer's motor system: a TMS study

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Abstract

Several transcranial magnetic stimulation (TMS) studies have reported facilitation of the primary motor cortex (M1) during the mere observation of actions. This facilitation was shown to be highly congruent, in terms of somatotopy, with the observed action, even at the level of single muscles. With the present study, we investigated whether this muscle-specific facilitation of the observer's motor system reflects the degree of muscular force that is exerted in an observed action. Two separate TMS experiments are reported in which corticospinal excitability was measured in the hand area of M1 while subjects observed the lifting of objects of different weights. The type of action 'grasping-and-lifting-the-object' was always identical, but the grip force varied according to the object's weight. In accordance to previous findings, excitability of M1 was shown to modulate in a muscle-specific way, such that only the cortical representation areas in M1 that control the specific muscles used in the observed lifting action became increasingly facilitated. Moreover, muscle-specific M1 facilitation was shown to modulate to the force requirements of the observed actions, such that M1 excitability was considerably higher when observing heavy object lifting compared with light object lifting. Overall, these results indicate that different levels of observed grip force are mirrored onto the observer's motor system in a highly muscle-specific manner. The measured force-dependent modulations of corticospinal excitability in M1 are hypothesized to be functionally relevant for scaling the observed grip force in the observer's own motor system. In turn, this mechanism may contribute, at least partly, to the observer's ability to infer the weight of the lifted object.

Introduction

In social interactions, humans demonstrate the remarkable ability to understand and interpret the behaviour of other people. Recently, neuroscience has increasingly focussed on the role of the observer's motor system during action understanding (Rizzolatti & Craighero, 2004). This line of research was strongly influenced by single-cell recordings in monkeys, demonstrating the existence of 'mirror neurons', which were shown to respond both when a monkey performs a certain action and when it observes another person performing the same action (Di Pellegrino *et al.*, 1992). In humans, several neuroimaging and neurophysiological studies have identified the inferior frontal gyrus (IFG) as well as the parietal cortex to be key areas of the 'human mirror neuron system' (Grafton *et al.*, 1996; Decety *et al.*, 1997; Cochin *et al.*,

1998; Buccino *et al.*, 2001, 2004; Grezes *et al.*, 2003; Lui *et al.*, 2008). With transcranial magnetic stimulation (TMS), it was shown that parts of the primary motor cortex (M1) that control particular muscles become increasingly facilitated during the mere observation of actions involving these muscles (Fadiga *et al.*, 1995; Strafella & Paus, 2000). Moreover, corticospinal excitability of M1 reflects specific characteristics of observed actions. In addition to the robust finding that modulations of M1 excitability are strongly muscle specific (Borroni & Baldissera, 2008; Alaerts *et al.*, 2009), previous research also showed that modulations in M1 excitability are highly synchronized to the temporal dynamics of observed movements (Gangitano *et al.*, 2001; Borroni *et al.*, 2005; Montagna *et al.*, 2005) and lateralized to the contralateral hemisphere when right- vs. left-hand actions are observed (Aziz-Zadeh *et al.*, 2002). As such, it appears that visual-motor matching during observation is a highly specified process, such that different features of the observed actions are encoded by the observer's motor system.

All of the above parameters (muscular involvement, temporal dynamics, used effector) can be easily derived from robust differences in the kinematics of the observed movement. However, until now it is unclear whether features that are less salient in the kinematic signal, such as the force requirements of an observed lifting action, are also

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matched to the observer's motor system. Some behavioural studies already indicated that the weight of a box (which strongly relates to the force needed to lift it) can be inferred quite accurately by observing another person lifting it (Runeson & Frykholm, 1981; Bingham, 1987). Interestingly, however, Hamilton *et al.* (2004) showed that performing an action, specifically holding a box, systematically biases the observers' psychophysical judgements of the weight of a box lifted by another person (Hamilton *et al.*, 2004). Based on this finding, it was hypothesized that overlapping neural systems for motor control and action observation may be recruited when observed and performed actions are processed simultaneously (Hamilton *et al.*, 2004). A subsequent functional magnetic resonance imaging (fMRI) study investigated the neural basis of this bias effect and, among the potential brain regions, the authors identified area M1 and the frontal node of the mirror system (IFG) as key sites of interaction between perceptual and motor processes (Hamilton *et al.*, 2006). The finding that this bias network extends to primary motor regions prompted the authors to speculate that simulation of observed weight-lifting actions can be a detailed motor process, rather than a visual or conceptual pattern matching (Hamilton *et al.*, 2006). In a more recent fMRI study, the neural representation site of observed object lifting was explored again using a repetition suppression design. However, the involvement of both the IFG and M1 during the mere observation of weight lifting was not confirmed from this study (Hamilton & Grafton, 2007), such that the actual involvement of the motor system in 'simulating' observed weight lifting needs to be established further.

As TMS is known to be an excellent technique to assess modulations of corticospinal excitability at the level of M1 (Fadiga *et al.*, 2005; Hallett, 2007), the present study used this technique to explore excitability modulations in the observer's motor system during the observation of lifting objects with different weights. As such, the type of action (i.e. 'grasping and lifting the object') was always identical but the grip force varied according to the object's weight. If action observation involves a detailed motor matching process, we hypothesized the excitability of M1 to modulate according to the force exerted in the observed actions, such that perception of lifting heavy objects yields higher excitability responses compared with perceiving the lifting of light objects. This hypothesis was tested by two complementary experiments, performed in two different laboratories.

Materials and methods

Subjects

All subjects participated after providing informed consent, and all experimental protocols were approved by the University of Ferrara Ethical Committee (Experiment 1) and the local Ethics Committee for Biomedical Research at the KU Leuven (Experiment 2) in accordance to The Code of Ethics of the World Medical Association (Declaration of Helsinki; Rickham, 1964). All participants were right-handed, as assessed with the Edinburgh Handedness Questionnaire (Oldfield, 1971), and were naive about the purpose of the experiment. Eight subjects (five males, three females) aged between 20 and 32 years (mean: 22 years) participated in Experiment 1, conducted at the University of Ferrara, Italy. Twelve subjects (three males and nine females) aged between 21 and 35 years (mean: 23 years) participated in Experiment 2, conducted at the Katholieke Universiteit Leuven, Belgium.

Electromyographic (EMG) recordings and TMS

Surface EMG was performed with Ag–AgCl surface electrodes placed over the muscle belly and aligned with the longitudinal axis of the muscle. In Experiment 1, EMG activity was recorded from the right first dorsal interosseous (FDI) finger muscle, an intrinsic hand muscle acting as agonist for precision grip. In Experiment 2, EMG activity was recorded simultaneously from the right opponens pollicis (OP) thumb muscle, and wrist flexor (FCR) and extensor (ECR) carpi radialis muscles.

Focal TMS was performed by means of a 70-mm figure-of-eight coil connected to a Magstim 200 stimulator (Magstim, Whitland, Dyfed, UK). The coil was positioned over the left hemisphere, tangentially to the scalp, with the handle pointing backward and laterally at 45° away from the mid-sagittal line, such that the induced current flow was in a posterior–anterior direction, i.e. approximately perpendicular to the central sulcus. An articulated arm (Manfrotto, Italy) was used for coil positioning in Experiment 1. A point, located 5 cm lateral to the vertex on the interaural line, was used as a reference point to localize the optimal scalp position for stimulation of the hand area of M1 (Mills & Nithi, 1997). TMS stimulations were randomly applied over each point of a small grid centred on this reference point, and the optimal scalp position was defined as the position from which motor-evoked potentials (MEPs) with maximal amplitude were recorded in, respectively, the right FDI (Experiment 1) or right OP (Experiment 2) muscles. The resting motor threshold (rMT) was defined as the minimal intensity evoking 5 MEPs out of 10 consecutive stimuli with an amplitude above or equal to 50 μV in the targeted muscle (Rossini *et al.*, 1994). Stimulation intensity was set at, respectively, 120% (Experiment 1) or 130% (Experiment 2) of the rMT for all experimental trials. In Experiment 2, stimulation settings were prioritized for the OP muscle, but MEPs were simultaneously obtained for the FCR and ECR muscles. Simultaneous measurements from the FCR and ECR are assumed to be satisfactorily similar, due to the partial overlap of representations of finger and forearm flexor and extensor muscles (Scheiber, 1990). In Experiment 1, EMG signals were band-pass filtered (50–1000 Hz), digitized (2000 Hz) and stored on a PC for off-line analysis. In Experiment 2, EMG signals were sampled at 5000 Hz (CED Power 1401, Cambridge Electronic Design, UK), amplified, band-pass filtered (30–1500 Hz) and stored on a PC for off-line analysis. Signal Software (2.02 Version, Cambridge Electronic Design, UK) was used for TMS triggering and EMG recordings.

General procedure

Experiment 1: observation of object lifting with a precision grip (live actions)

Participants were seated on a comfortable chair (dental chair type), their arms were stretched out on an arm support with their hand relaxed and pronated. They faced a small stage with black floor and background. A square metallic platform aligned with the subject's sagittal plane supported the target object on which action was performed. The actor was seated fully visible on the front right of the participant and acted with his right hand on the target object, parallel to the subject's frontal plane. The observed actor reached to grasp the object with his right hand, lifted it, held it few seconds and then replaced it at its initial position. The two objects presented (Fig. 1A) were of different shape and explicitly of different weight despite that they both could be grasped by opposing the tips of the thumb and index finger (precision grip) thanks to a common handle. The first object ('Light') was a 10 g piece of ribbon cable that was held erected by individualizing the wires at the lower extremity of the ribbon. The other object ('Heavy') was a 500 g brass balance weight with a handle made of the same ribbon cable used for the light object. In each trial, the actor's hand initially laid pronated on the table, pushing with the fingertips a hidden switch placed at about 20 cm from the object
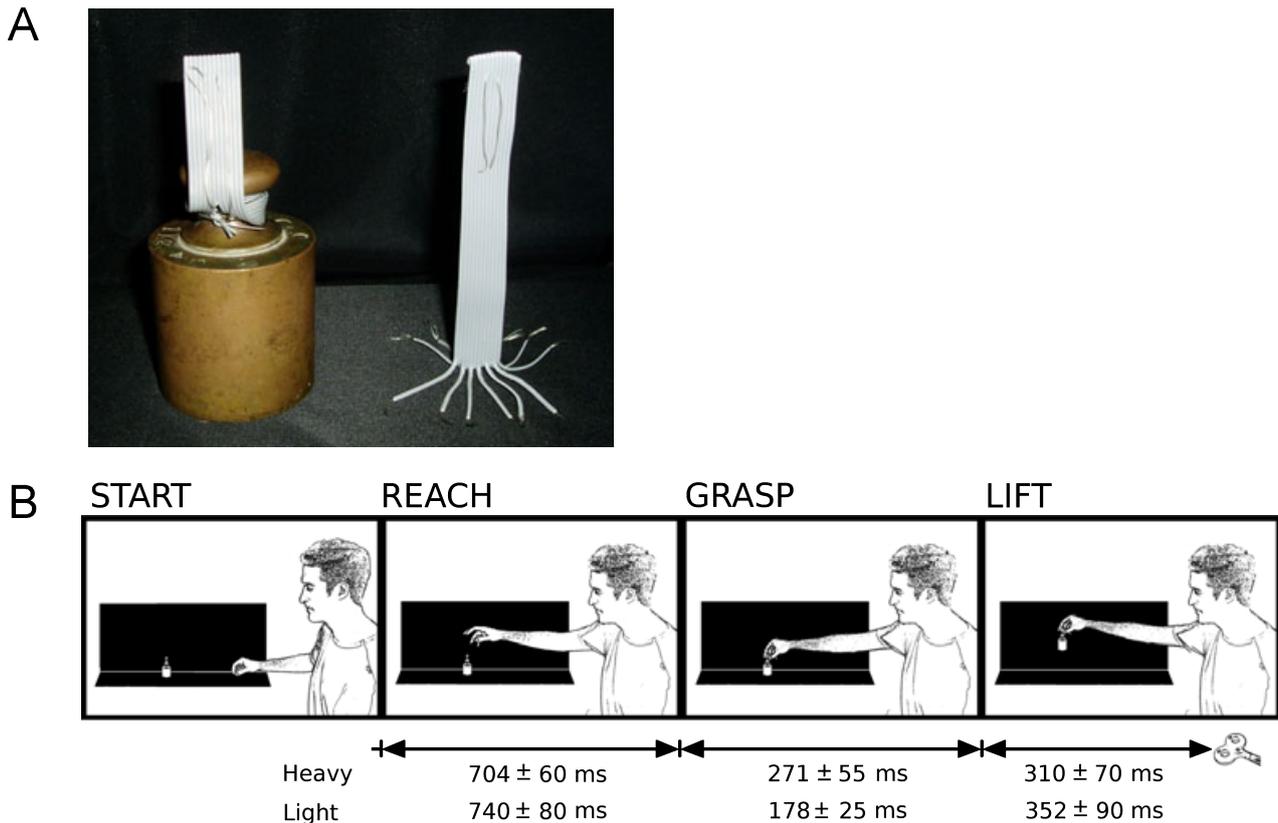
FIG. 1. Experimental stimuli of Experiment 1. (A) Picture of the two objects grasped and lifted in front of the subject. The 500 g 'Heavy' object (left) was a typical brass balance weight. The 10 g 'Light' (right) object was a piece of ribbon cable. Both objects were grasped using the same grip hand shape. (B) Illustration of events sequence during observation of the reach–grasp–lift action executed upon the heavy object: the actor started hand pronated, then reached to the object, grasped it with precision grip, lifted it and held it over the table for 1 s. A TMS pulse was delivered during the lifting phase. The time-line provides the averaged intervals (mean ± STD, $n = 7$) between the main task events (button release, hand–object contact, lift onset, TMS pulse) for action upon both the heavy and the light object.

(Fig. 1B). One of the two objects was then placed on the platform. A vocal warning ('pronto') was provided to signal the incoming of a new trial. The contact time of the actor's fingers with the object and the lifting latency were provided, respectively, by an electric circuit switched on by the contact between both fingers and the object's handle and switched off by the separation between the object and the metallic platform. Each of the two objects was presented 15 times, with presentation order randomized within subjects. A single TMS pulse was delivered 750 ms after the hand crossed an optic beam placed just in front of the target object. This latency was chosen empirically to ensure that the TMS pulse actually occurred during the lifting phase (Fig. 1B). In total, 30 MEPs were recorded for each subject. Before the experimental session, subjects could see the objects and were allowed to experience their respective weight.

Experiment 2: observation of object lifting with a whole-hand grip (video clips)

Participants were seated in a comfortable chair in front of a Dell P992 monitor (resolution, 1024 × 768 pixels; refresh frequency 60 Hz) on which video clips (Audio-Video Interleaved; AVI) were displayed with a frame rate of 25 Hz (or frames/s). The experimental video clips showed the target object and the model's right hand that acted upon it. The model's hand entered the scene from the subject's right side, reached to grasp the object and subsequently lifted it out of the scene in the vertical plane (Fig. 2). The three target objects were plastic drinking bottles with a weight of, respectively, 0 kg (empty), 1 kg (half full) and

2 kg (full). All bottles were grasped with a whole-hand grip, i.e. by using the thumb and hand palm (Fig. 2). Additionally, a control video clip was presented to the subjects showing only an empty white background without any overt action (i.e. Baseline). All video clips lasted for 10 s. Each of the four video clips was presented 20 times in blocks of four, with the block presentation order randomized within and across subjects. During the presentation of each video clip, a single TMS pulse was delivered at a random time point during the bottle-lifting phase (Fig. 2). For each video, TMS stimulation timing corresponded to the time interval at which the bottle was vertically lifted from the table surface with a displacement of 3–12 cm. Video presentation timing was controlled by Blaxton Video Capture software (South Yorkshire, UK). In total, 80 MEPs were recorded from each subject. Before the experimental session, all video clips were presented to the subjects in order to familiarize them with the experimental stimuli. During the session, they were instructed to keep their hands and forearms as relaxed as possible and to pay full attention to the video presented, such that they could report the type of video after each trial.

The main differences between the observational paradigms used in Experiments 1 and 2 regard: (i) the observation of a precision grip (Experiment 1) or of a whole-hand prehension (Experiment 2); (ii) the recording of one muscle only (FDI; Experiment 1) or of three muscles (OP, FCR and ECR; Experiment 2); (iii) the comparison of two weights (Experiment 1) or of three weights (Experiment 2); and (iv) the involvement of a real agent performing the movement (Experiment 1) or the use of videos (Experiment 2). Although both types of stimuli (i.e. real actions or video-taped actions) are known to induce a

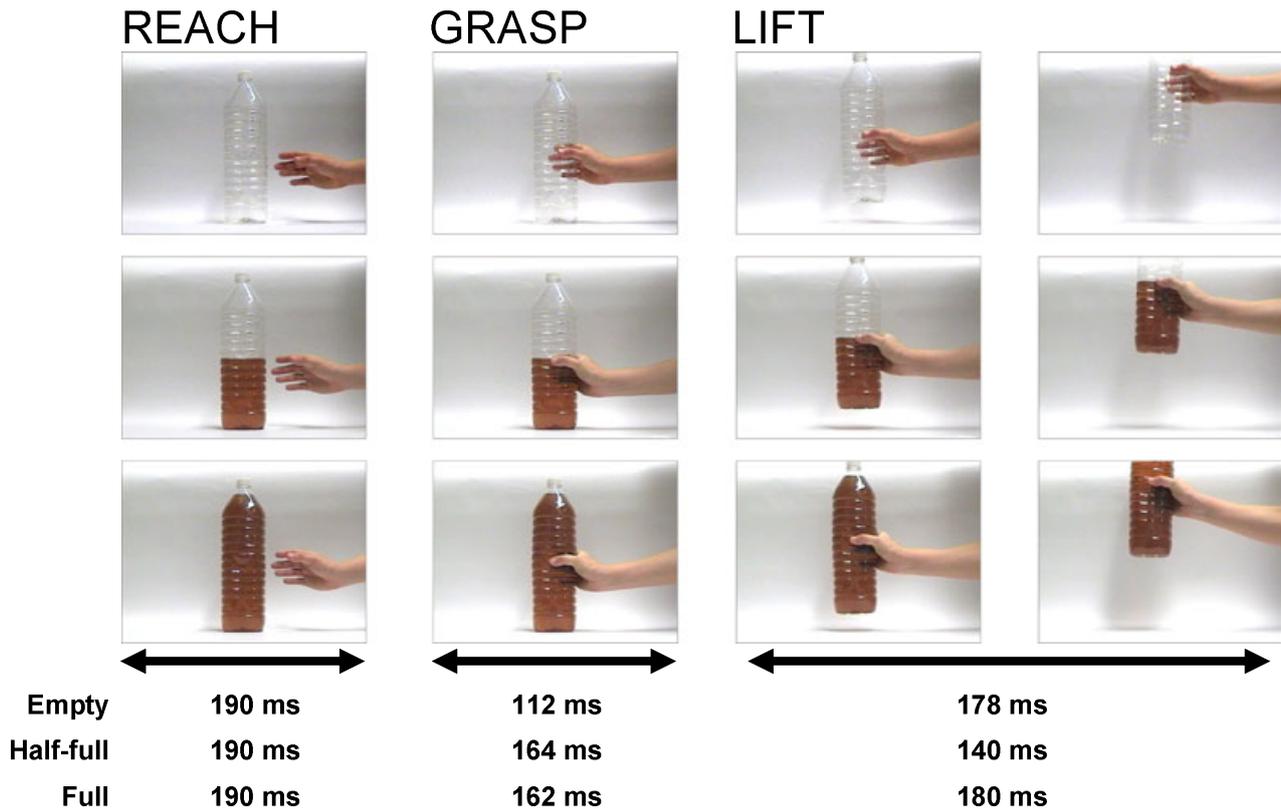|	REACH	GRASP	LIFT
Empty	190 ms	112 ms	178 ms
Half-full	190 ms	164 ms	140 ms
Full	190 ms	162 ms	180 ms

FIG. 2. Experimental stimuli of Experiment 2. The experimental video clips showed a reach–grasp–lift action of a plastic drinking bottle with three different weights, i.e. an empty (0 kg), a half full (1 kg) and a full (2 kg) bottle. The actor entered the scene from the right side, reached to the object, grasped it with a whole-hand grip and lifted it out of the scene in the vertical plane. TMS pulses were delivered at random time points during the bottle-lifting phase.

reactivation of M1, it may be worth mentioning that reactivations were shown to be more salient for observing real actions compared with video-taped actions (Jarvelainen *et al.*, 2001).

Data reduction and analysis

From the EMG data, peak-to-peak amplitudes of the MEPs were determined. Because EMG background activation is known to modulate the MEP amplitude (Devanne *et al.*, 1997; Hess *et al.*, 1987), pre-stimulation EMG was assessed in both experiments by computing root-mean-square error scores (RMSE) across a 50-ms interval prior to the TMS stimulation. For each subject and for each muscle separately, mean and standard deviation of the EMG background scores were computed over all trials. Trials for which EMG background was above the mean + 2.5 standard deviation were removed from the analysis. Trials for which the MEP amplitude was inferior to the mean EMG background were also discarded. Finally, extreme peak-to-peak amplitudes values were considered as outliers and removed from the analysis when they exceeded $Q3 \pm 1.5 \times (Q3 - Q1)$, with Q1 being the first quartile and Q3 the third quartile computed over the whole set of trials for each subject (Electronic Statistics Textbook, 2007, StatSoft, Tulsa, USA). Following these three criteria in Experiment 2, only 4% of all trials (of all subjects) were discarded from the analyses for each muscle (OP–FCR–ECR). In Experiment 1, one subject was discarded, due to 80% of bad trials in one of the observation conditions. From the remaining subjects, 13% were discarded in total.

MEPs were normalized relative to the subjects' maximal MEP amplitude (measured over all trials and conditions; MEP/MEP$_{\text{MAX}}$). To analyse modulations in background EMG across observation conditions, RMSE scores were normalized accordingly (RMSE/RMSE$_{\text{MAX}}$).

Statistics

In Experiment 1, paired *t*-tests were used to compare peak-to-peak MEP amplitude data recorded during the observation of the heavy and light weight-lifting. In Experiment 2, MEP amplitude data recorded during the observation of the experimental video clips were subjected to a two-way analysis of variance (ANOVA) with repeated measures, with the within factors 'Muscle' (OP, FCR, ECR) and 'Grip force' (Empty, Half Full, Full). All significant interactions were analysed further using Fisher LSD *post hoc* tests (Statistica 7.0, StatSoft, Tulsa, USA). Similar statistical analyses were applied to the background EMG data (normalized RMSE scores) to assess whether the MEP amplitude scores were confounded by modulations in background EMG.

Measurements of muscle activity during the execution of object lifting with a whole-hand grip

Five subjects (age range 23–30 years; three females, two males) participated in an additional experiment to record the corresponding muscle activity during the actual execution of the whole-hand reach–grasp–lift actions of Experiment 2. The subjects participating in the action observation TMS experiment were not the same subjects participating in this additional action execution experiment.

Subjects were instructed to observe a video displaying a grasp–lift action and to simultaneously perform the same action in synchrony

with the video. The video showed the whole-hand grasp and lift of drinking bottles with three different weights, i.e. an empty (0 kg), a half full (1 kg) and a full (2 kg) bottle (Fig. 2). During execution, EMG was simultaneously recorded from the right OP thumb and FCR/ECR wrist muscles. Each subject performed the three actions 15 times. In 12 additional trials, the EMG was recorded during maximal voluntary contraction (MVC) of each muscle. Peak EMG amplitudes were calculated within a short time-interval of 40 ms during the lifting of the bottle (Fig. 2). EMG changes were expressed as the percentage of subjects' muscle-specific MVC scores (Ankrum, 2000).

Results

Experiment 1: observation of object lifting with a precision grip

During the observation of object lifting with a precision grip, normalized MEP amplitudes revealed a systematic modulation relative to the force requirements of the observed scene (Fig. 3). Figure 3A and B presents a representative example of individual and averaged MEPs for the two conditions. A clear difference in MEP amplitude is visible for this particular subject. In fact, for six out of seven subjects, MEP amplitude scores were higher during observation of heavy object lifting compared with light object lifting, as shown by the individual regression lines in Fig. 3C. At the group level ($n = 7$), this consistent trend led to significantly higher normalized MEP amplitudes for the heavy compared with the light weight observation condition ($t = 2.8$, $P = 0.031$; Fig. 3D).

A paired *t*-test computed on the background EMG data (normalized RMSE scores) confirmed that the EMG background was not significantly different in the two conditions ($t = 0.972$, $P = 0.369$), indicating that experimental results are not likely explained by a modulation in background EMG.

Experiment 2: execution of object lifting with a whole-hand grip

During the execution of object lifting with a whole-hand grip, OP and ECR muscles were found to be more involved in the action compared with the FCR muscle (Fig. 4). Indeed, a consistent effect across subjects was found for the OP and ECR muscle (and to a lesser extent for the FCR muscle), indicating gradually higher muscle activity for executing the lifting of an empty, half full and full bottle (Fig. 4A).

These observations were further supported by the two-way ANOVA interaction between 'Muscle' (OP, FCR, ECR) and 'Grip Force' (Empty, Half Full, Full; $F_{4,16} = 3.22$, $P < 0.05$). Main effects of 'Muscle' ($F_{2,8} = 4.91$, $P < 0.05$) and 'Grip force' ($F_{2,8} = 55.68$, $P < 0.001$) were also found. Moreover, *post hoc* analysis of the two-way interaction revealed that for the OP and ECR, all force levels were significantly different from one another, indicating that modulations in muscle activity as a function of object weight were more pronounced in the OP and ECR muscle, compared with the FCR muscle (Fig. 4B).

Experiment 2: observation of object lifting with a whole-hand grip

During the observation of object lifting with a whole-hand grip, normalized MEP amplitudes revealed a systematic modulation relative to the force requirements of the observed scene (Fig. 5). Moreover, force-related modulations in MEP responses were exclusively found for muscles involved in the execution of the observed action, as shown

for an exemplary subject in Fig. 5A. Indeed, consistent results across most subjects were only found in the OP and ECR, but not in the FCR (Fig. 5B), indicating minimal MEP responses for the baseline condition (observing a white background without any overt action) and gradually higher MEP responses for observing the lifting of an empty, half full and full bottle.

These observations were further supported by the two-way ANOVA interaction between 'Muscle' (OP, FCR, ECR) and 'Grip Force' (Empty, Half Full, Full; $F_{4,44} = 3.46$, $P < 0.05$). A main effect of 'Muscle' ($F_{2,22} = 3.81$, $P < 0.05$), but not of 'Grip Force' ($F_{2,22} = 2.37$, $P = 0.117$) was also found. *Post hoc* analysis of the two-way interaction revealed that MEP responses evoked from the OP muscle were significantly higher for observing the lifting of the half full or full bottle compared with observing the empty bottle (both, $P < 0.01$; Fig. 5B). MEP scores yielded from the ECR muscle showed a similar modulation (empty vs. half full, $P = 0.05$; empty vs. full, $P = 0.007$). In the FCR, on the other hand, no differences in MEP scores were measured for observing the different weight lifting ($P > 0.2$; Fig. 5C). As such, MEP modulations measured during the observation of weight lifting nicely corresponded to the muscle activation pattern found during movement execution.

The background EMG was generally small and condition-specific modulations were minimal. This was tested by conducting a similar two-way ANOVA analysis (within factors 'Muscle' and 'Grip Force') to the corresponding background EMG data (normalized RMSE scores). None of the main or interaction effects reached significance (all $F < 1.5$, $P > 0.21$), which indicated that the MEP amplitude scores were not confounded by modulations in background EMG.

Discussion

With the present TMS experiments, we tested whether the observer's motor system reflects the force requirements of observed actions. Our results indicated that, in accordance to previous findings, corticospinal excitability modulations during action observation are specific for those muscles involved in the execution of the observed action, and that this muscle-specific modulation is influenced by the force requirements of the observed actions, such that higher corticospinal excitability was found for the perception of lifting heavy objects compared with perceiving the lifting of light objects.

Perception of object lifting excites the human corticomotor system in a force-related way

In two separate experiments, carried out in two distinct laboratories, we examined whether the force requirements of an observed action are encoded in the observer's motor system during the process of visual-motor matching. Addressing the same research question, the two experiments differed mutually according to some set-up-related aspects. First, in Experiment 1, 'live' actions were presented to the observing subjects, whereas in Experiment 2 'video' presentation was used. Second, although both experiments presented (right-hand) 'grasp–lift' actions of different object weights, Experiment 1 showed a 'precision grip' (i.e. opposing the tips of the thumb and index finger), whereas Experiment 2 showed a 'whole-hand grip' (i.e. using the thumb and all fingers). Consequently, the type of the 'to-be-grasped objects' also differed, particularly with respect to the weight ranging from 0 to 500 g in Experiment 1, and from 0 to over 1000–2000 g in Experiment 2. However, despite these differences, both experiments established the same robust results, namely a facilitation of the observer's motor system, which corresponded to the force

A

Light   Heavy

All trials

0.25
n.u.
0.01s
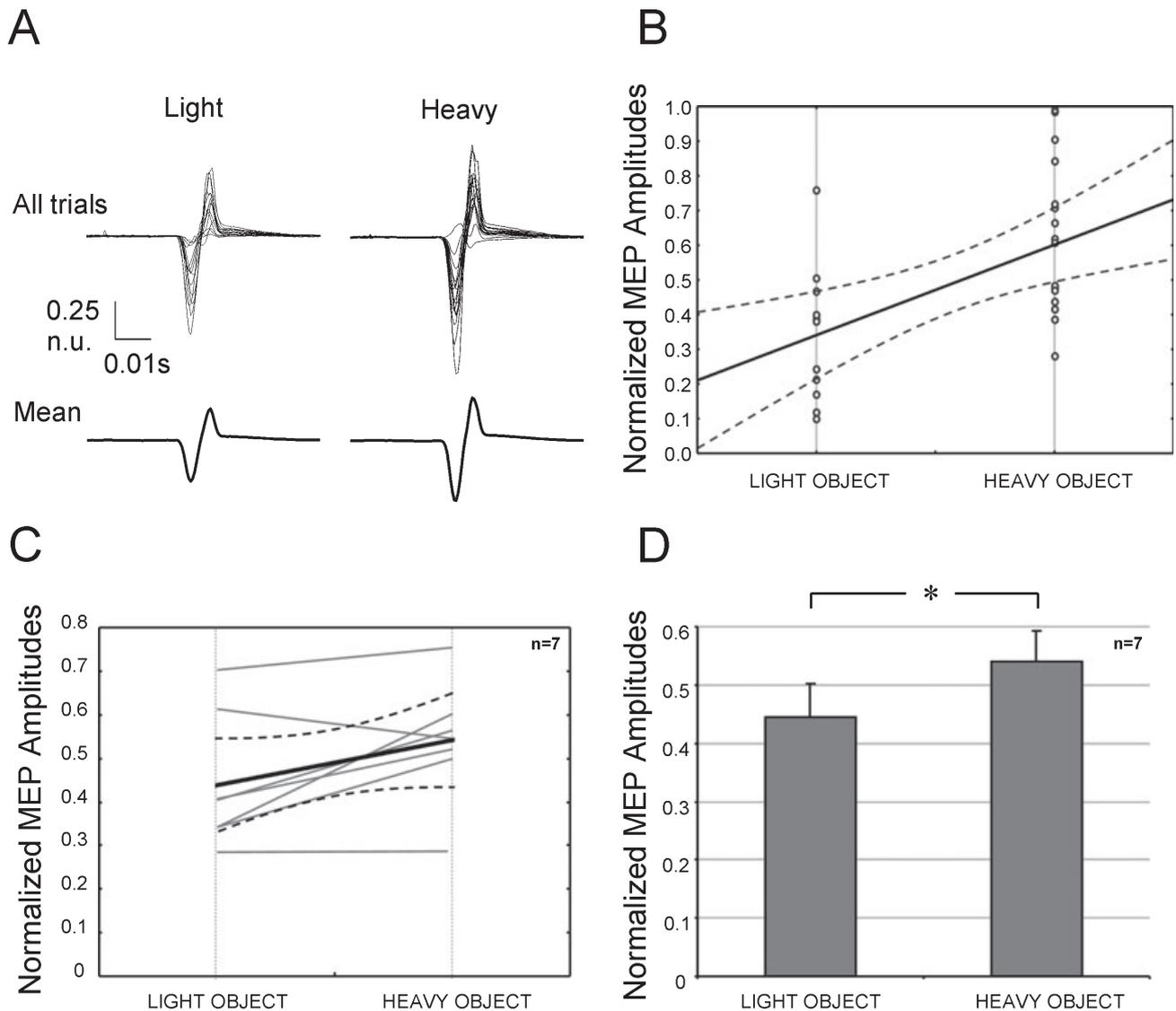
Mean

B

C

D

FIG. 3. Results of Experiment 1: observation of object lifting with a precision grip. Peak-to-peak motor-evoked potential (MEP) amplitudes were recorded from the FDI muscle during observation of lifting the 'Heavy' and the 'Light' object. (A) A representative example of individual MEPs recorded from the FDI muscle during observation of lifting a light and heavy object. (B) Representative example of individual MEP scores (# 15/condition). A regression line is fitted to the MEP scores (grey dots) recorded from the light and heavy observation conditions. Dashed black lines denote 95% confidence intervals. (C) Regression lines for all individual subjects (grey; $n = 7$) and the group regression line (black) across observation conditions. Dashed black lines denote 95% confidence intervals. Observing how the heavy object was lifted evoked larger mean MEP scores than observing how a light object was lifted, as indicated by a positive correlation (mean Pearson $r = 0.39$, individual r ranged from -0.13 to 0.55). (D) Averaged values ($n = 7$) of peak-to-peak amplitude MEPs for each experimental observation condition. Asterisks indicate significant differences between conditions (*$P < 0.05$). Vertical lines denote standard errors.

requirements of the observed lifting actions. As such, finding similar results in two separate but complementary experiments (performed in two different laboratories) indicates the robustness and generalizability of the described effects. Experiment 2 additionally confirmed that the force-related facilitation of M1 was highly specific to the actual muscles used in the observed lifting actions. In this view, we extend previous findings by showing that observation-induced facilitation of the observer's M1 reflects the muscular requirements of the observed movement, not only in terms of the muscle used in the observed motion, but also in terms of the force that is produced in the particular muscle. Thus, observation-to-execution mapping includes also some dynamical features of motor control, such as grip force.

The present findings reveal also interesting insights on 'how accurate' force requirements are mapped within the observer's motor system. From the execution experiment (Experiment 2) it was shown that the muscle activity in the OP and ECR muscle was substantially higher for lifting a full compared with lifting a half full bottle. However, the elicited corticospinal responses differed only moderately between the 'full' and 'half full' observation condition, and this difference did not reach statistical significance (Experiment 2). This finding suggests that force encoding was more accurately represented during movement execution than movement observation, particularly when relatively large forces were applied. Similar results were revealed by a weight discrimination study, whereby subjects observed grasp–lift actions of small objects with a weight range of 50–850 g (increasing with steps of 200 g; Hamilton et al., 2004). Even though the objects' weights were discriminated successfully, responses were fitted best by a quadratic regression, suggesting a ceiling effect for
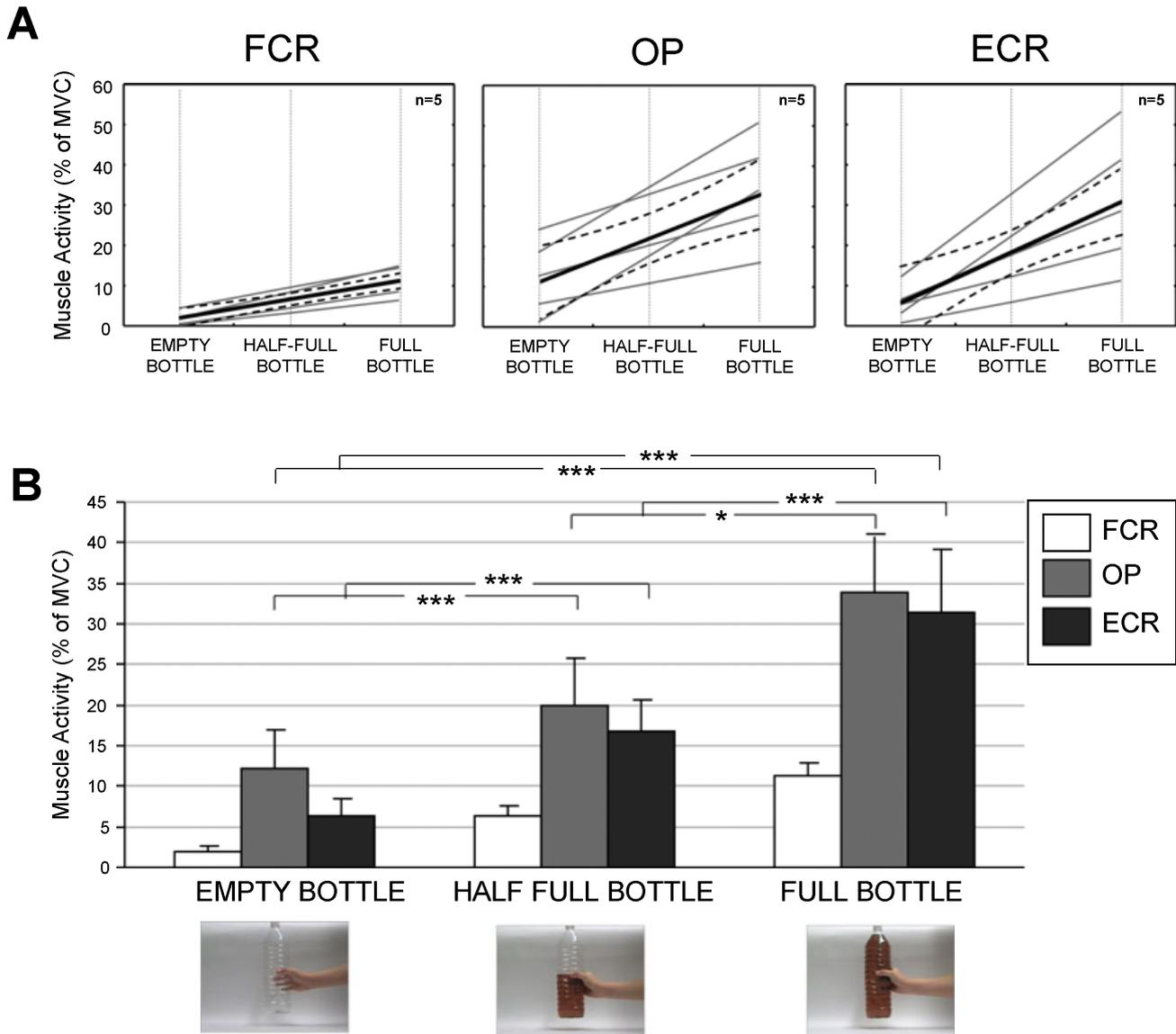
A

B

FIG. 4. Results of Experiment 2: execution of object lifting with a whole-hand grip. Muscle activity (EMG) was recorded from the opponens pollicis (OP), extensor carpi radialis (ECR) and flexor carpi radialis (FCR) muscles during the execution of object lifting with a whole-hand grip (expressed as a percentage of the subjects' maximal voluntary contraction; MVC). Three different weights were lifted: an empty (0 kg), a half full (1 kg) and a full (2 kg) bottle. (A) For each muscle, the individual subjects' regression lines (grey; $n = 5$) and the group regression line (black) are displayed across execution conditions (i.e. lifting of empty, half full, full bottle). Dashed black lines denote 95% confidence intervals. Executing the lifting of an empty, half full and full bottle evoked gradually larger muscle activity in all muscles, as indicated by positive correlations (individual Pearson $r > 0.60$). (B) Averaged values ($n = 5$) of muscle activity (EMG) are displayed for each execution condition and muscle. Asterisks indicate significant differences between conditions ***$P < 0.001$; *$P < 0.05$. Vertical lines denote standard errors.

judging the highest weights (850 g). As such it can be tentatively hypothesized that a similar ceiling effect is reflected by M1 facilitation when considerably 'high' grip forces were observed. However, it should be noted that other tasks such as weight discrimination based on the observation of whole-body lifting actions did not exhibit a similar ceiling effect. Instead, a linear relationship was found when lifting actions were observed for weights ranging from 3 to 27 kg (increasing with steps of 6 kg; Runeson & Frykholm, 1981). These differences may relate to the fact that the optimal weight discrimination range might be different between muscles that develop relatively 'weak' maximal contractions (e.g. distal hand muscles involved in fine-grip force tuning) and muscles developing considerably 'stronger' maximal contractions (e.g. proximal arm muscles involved in whole-body lifting actions).

Functional significance of force-related excitability modulations in M1

Although perception and action were traditionally considered to be two distinct processes, a number of studies, using a variety of techniques, demonstrated 'mirror' activity in motor areas during the mere perception of others' action (Rizzolatti & Craighero, 2004; Fadiga *et al.*, 2005). However, to date, different hypotheses exist concerning the role of this observation-to-execution matching system.

On the one hand, it is proposed that mirror neurons contribute solely to motor planning or action preparation. Under this 'motor' hypothesis, activation of motor areas during movement observation is principally a motor resonant phenomenon (Jacob & Jeannerod, 2005). However, the most widely accepted hypothesis argues that mirror
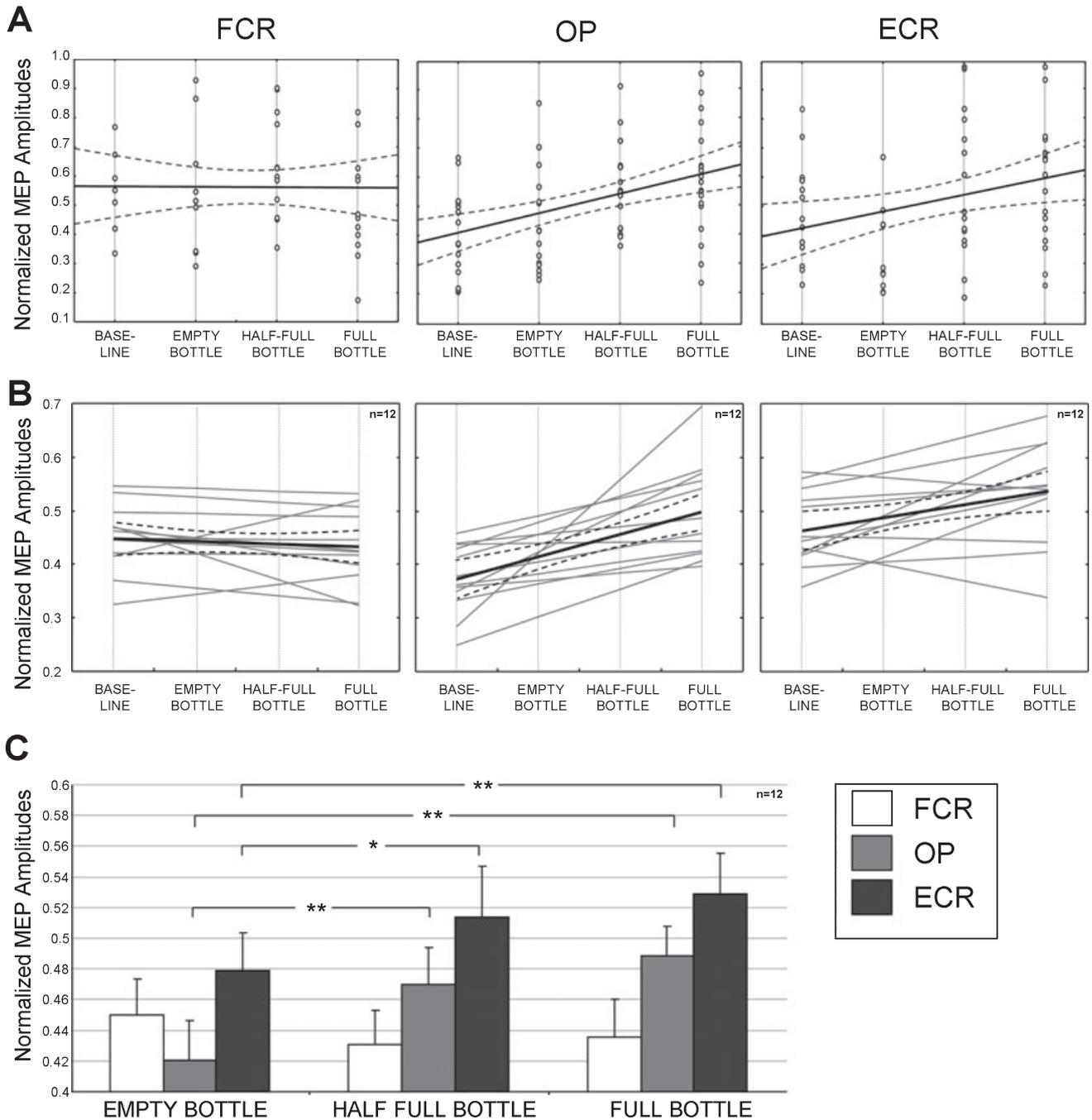
FIG. 5. Results of Experiment 2: observation of object lifting with a whole-hand grip. Peak-to-peak motor-evoked potential (MEP) amplitudes were recorded from the opponens pollicis (OP), extensor carpi radialis (ECR) and flexor carpi radialis (FCR) muscles during the observation of a baseline video (displaying a white background without any overt action), and during the observation of three experimental videos displaying object lifting with a whole-hand grip. Lifting of three different weights was observed: an empty (0 kg), a half full (1 kg) and a full (2 kg) bottle. (A) Representative example of individual MEP scores (# 20/condition). For each muscle, a regression line is fitted to the MEP scores (grey dots) recorded from the different observation conditions (i.e. baseline and three experimental videos). Dashed black lines denote 95% confidence intervals. (B) Regression lines for all individual subjects (grey; $n = 12$) and the group regression line (black) are displayed for each muscle across observation conditions. Dashed black lines denote 95% confidence intervals. A positive linear correlation across conditions was only displayed for the OP (mean Pearson $r = 0.49$, individual r ranged from 0.01 to 0.60) and ECR muscle (Pearson $r = 0.26$, individual r ranged from −0.13 to 0.38), not for the FCR muscle (Pearson $r = -0.08$, individual r ranged from −0.32 to 0.21). (C) Averaged values ($n = 12$) of peak-to-peak amplitude MEPs are displayed for each experimental observation condition and each muscle. Asterisks indicate significant differences between conditions **$P < 0.01$; *$P < 0.05$. Vertical lines denote standard errors.

neurons provide a representation of actions that allows the observer to 'automatically resonate' to observed actions in his own motor repertoire system, in order to understand or interpret the actions made by others (Gallese et al., 1996; Iacoboni et al., 2005; Craighero et al., 2007; Rizzolatti & Fabbri-Destro, 2008). In accordance to the latter

hypothesis, we tentatively propose that the reported force-dependent modulations of M1 excitability are functionally relevant for scaling the observed grip force in the observer's own motor system, i.e. by mapping the force requirements of the observed action in a muscle-centred coordinate frame within M1. In everyday life, observing how

an unknown object is lifted by others often allows the observer to predict quite accurately the appropriate grip force needed to prevent slip upon acceptance of the object. Here, we hypothesize that a perception-induced 'force-scaling' mechanism in the observer's own motor system may contribute, at least partly, to this remarkable ability. Although we did not formally assess the individual subjects' ability to judge the produced grip force, informal debriefing confirmed that all subjects were conscious of the fact that the lifted objects differed in their respective weights, and accordingly that a differential level of grip force was exerted to lift them. Nonetheless, to firmly establish the functional contribution of M1 in action understanding, it should be interesting to explore whether grip force perception is affected by disruptive TMS at the level of M1.

Potential neural mechanisms underlying the force-related excitability modulations in M1

The actual execution of successful grasps and lifts of objects involves several neuronal mechanisms, some of them being concerned with fine-tuning the grip force of the grasping fingers, and others with the transformation of object properties into motor actions (Castiello, 2005). In this respect, the IFG is suggested to be involved in selecting the most appropriate 'motor prototype', such as the type of grip that is effective in interacting with the target object (Fagg & Arbib, 1998; Davare *et al.*, 2008), whereas the actual fine-tuning of grip force has been shown to rely strongly on M1 activity (Muir & Lemon, 1983; Lang & Schieber, 2004). Interestingly, there are several indications that similar brain areas may be involved during the mere perception of object lifting. Indeed, a number of studies convincingly demonstrated that the IFG is not only involved during action execution, but also during the mere observation of actions, such that it is considered to be a key area of the human mirror neuron system (Rizzolatti *et al.*, 1996; Grafton *et al.*, 1996; Nishitani & Hari, 2000; Johnson-Frey *et al.*, 2003; Fazio *et al.*, 2009). More specifically, in the context of observing the lifting of different weights, an elegant study by Pobric & Hamilton (2006) demonstrated that perceptual weight judgements depend significantly on activity within the IFG, i.e. disruptive rTMS at this site impaired judgements of the weight of a box lifted by another person, but not judgements on the weight of a bouncing ball, and rTMS at a control site did not have this effect (Pobric & Hamilton, 2006). Consistently, a study using fMRI also identified the IFG as well as M1 to be involved during perceptual weight judgement (Hamilton *et al.*, 2006). Considering that IFG is strongly connected to M1 (Shimazu *et al.*, 2004; Dum & Strick, 2005), it can be argued that the measured force-dependent facilitation of M1 is a result of cortico-cortical projections from IFG mirror neurons. To date, the actual role of M1 in the context of movement observation is still debated. On the one hand, M1 might simply be 'co-activated' with IFG, thereby representing the same information as IFG. Alternatively, however, it is argued that M1 could play a more functional role in movement observation by translating and representing the observed movement features in terms of muscle-related coordinates (Kilner & Frith, 2007; Lepage *et al.*, 2008; Pineda, 2008; Alaerts *et al.*, 2009). Therefore, in relation to the studies cited above, we suggest that, in the present experiment, IFG might be occupied with representing 'motor prototypes' (e.g. the type of grip), whereas M1 would be occupied with translating this information into 'movements', i.e. to map the types of recruited muscles as well as the level of force they produce.

Importantly, activity in IFG during weight judgement seems to rely predominantly on the general 'kinematics' of observed lifting actions,

and not on object-related information about to-be-grasped objects (lifted boxes were identical in the study of Pobric *et al.*, 2006). However, considering that 'object-related' cues were highly salient in the present experiments (e.g. the filling degree of the bottle in Experiment 2, or the type of material in Experiment 1), it can be speculated that an alternative mechanism, involving the recruitment of stored internal representations of object properties, may be operating here. Indeed, several previous studies have indicated that the motor system can store and recall information on object dynamics to predict the grip forces that will arise when acting on objects (Flanagan *et al.*, 2006). Accordingly, inputs from other brain areas, involved with the representation of object dynamics, may have driven the observed force-related modulation in M1. The parietal node of the mirror system, namely the intraparietal sulcus (IPS), may be a good candidate in mediating this effect. More specifically, in a series of fMRI studies by Grafton and Hamilton, the IPS was identified to be a key area in representing different target objects during action observation (Hamilton & Grafton, 2006; Grafton & Hamilton, 2007). In addition, a recent fMRI experiment showed that the anterior part of the IPS is also responsive to the passive viewing of graspable 3D objects, further indicating a role for this parietal region in adapting motor commands to object properties (Cavina-Pratesi *et al.*, 2007). However, the observation of different object weights alone appeared to be inefficient in triggering force-related excitability modulations in M1 (Leuven group, preliminary TMS work), suggesting that 'the action upon the object' is necessary to trigger the encoding of force requirements in the motor system. Another ongoing study (Ferrara group) also suggests that the force-related modulation found here is more dependent on 'motion-related' cues than on explicit or implicit object-related cues. Future experiments should confirm the relative contribution of object information and purely motion-related features in mediating the force-related responses.

In summary, the present study provides some exciting new evidence that resonant activity in motor areas is highly specified to map different features of observed actions. More specifically, data convincingly indicated that observation-induced facilitation of the observer's M1 reflects the muscular requirements of the observed movement, not only in terms of the muscle used in the observed motion, but also in terms of the force that is produced in the particular muscle.

Abbreviations

ECR, extensor carpi radialis; EMG, electromyographic; FCR, flexor carpi radialis; FDI, first dorsal interosseous; fMRI, functional magnetic resonance imaging; IFG, inferior frontal gyrus; IPS, intraparietal sulcus; M1, primary motor cortex; MEP, motor-evoked potential; MVC, maximal voluntary contraction; OP, opponens pollicis; RMSE, root-mean-square error scores; rMT, resting motor threshold; TMS, transcranial magnetic stimulation.

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