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 report that viewing other's actions facilitates the neural representation site of the onlooker's muscles that are recruited during the actual execution of the observed action. 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 corticomotor excitability was measured in the hand area of the primary motor cortex (M1) while subjects observed the lifting of objects with 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, activity of M1 was shown to modulate in a muscle-specific way, such that only those parts of M1 that control the specific muscles used in the observed lifting action, become increasingly facilitated. Moreover, the muscle-specific facilitation pattern of M1 was shown to modulate in accordance to the force requirements of the observed actions, such that corticomotor excitability was considerably higher for observing heavy object lifting compared to light object lifting. Overall, these results indicate that observed object grasping, requiring different force levels, is mirrored onto the observer's motor system in a highly muscle-specific manner, as measured in M1.

The measured force-dependent modulations of corticomotor activity in M1 are hypothesised to be functionally relevant for the observer's ability to infer the observed grip force and consequently 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 is increasingly focussing on the role of the observer’s motor system during action understanding (Rizzolatti & Craighero 2004). This possibility comes from results of 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;Grezes et al., 2003;Buccino et al., 2004;Lui et al., 2008). In addition, with transcranial magnetic stimulation (TMS) it was shown that parts of 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, M1-excitability modulations reflect specific characteristics of observed actions: Next to the robust finding that modulations of M1 are strongly muscle-specific (Borroni & Baldissera 2008;Alaerts et al., 2009a;Alaerts et al., 2009b), previous research also showed that M1 activations are highly synchronized to the temporal dynamics of an observed movements (Gangitano et al., 2001;Borroni et al., 2005;Montagna et al., 2005) and lateralized to the contra-lateral hemisphere when right- versus 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 in which 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 largely unclear whether features which are less salient in the kinematic signal, such as the force requirements of an observed lifting action, are also matched to the observer’s motor system. Some behavioural studies already indicated that the weight of a box (and consequently the force needed to lift it) can be inferred quite accurately by observing another person lifting it (Runeson & Frykholm 1981;Bingham 1987), and interestingly, some recent experiments demonstrated that the observer’s motor system might be involved in this task. More specifically, it was shown that the active lifting of weights interferes with concomitant weight judgement tasks (Hamilton et al., 2004). These findings suggest that similar force-related parameters are coded both in the motor plan and in the action representation evoked by the observation of the action. A following study localized the sites of interaction between perceptual and motor processes in several frontal and parietal areas and particularly in the IFG and M1 (Hamilton et al., 2006). However, activations in both regions were not confirmed during the mere observation of weight lifting (Hamilton & Grafton, 2007). As such, their actual involvement in weight perception needs to be established further.

As TMS is known to be very powerful in assessing activity modulations at the level of M1, the present study used this technique to explore possible force-related activity modulations in the observer's motor system during the observation of lifting objects with different weights.

In two separate experiments, performed in two laboratories, cortical excitability was measured in M1 during the observation of lifting objects with different weights. Thus, the type of action 'grasping and lifting the object' was always identical but the grip force varied according to the object's weight.

EXPERIMENT 1

Observation of object lifting with a precision grip

Experiment 1 was designed to test whether force requirements are encoded in the observer's motor system during observation of an actor lifting two different objects of explicit different weights, using a precision grip. Experiment 1 was run in Ferrara, Italy.

MATERIALS & METHODS

Subjects. Eight subjects (5 males, 3 females) with age between 20 and 32 (mean: 22) participated after providing informed consent. All experimental protocols were approved by the local ethics board 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.

Electromyographic recordings and TMS. Surface electromyography (EMG) was performed with Ag-AgCl electrodes placed according to a belly-tendon configuration. EMG activity was recorded from the right First Dorsal Interosseous (FDI) finger muscle, an intrinsic hand muscle acting as agonist for precision grip.

Focal transcranial magnetic stimulation (TMS) was performed by means of a 70 mm figure-of-eight coil connected to a Magstim 200 stimulator (Magstim). The coil was positioned over the left hemisphere, tangentially to the scalp with the handle pointing backward and medially 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 to keep coil position during the experiment. The optimal scalp position was defined as the position from which Motor Evoked Potentials (MEPs) with maximal amplitude were recorded in the right FDI muscle. The rest motor threshold (rMT) was defined as the lowest stimulus intensity evoking MEPs in the right FDI with an amplitude of at least 50µV in 5 out of 10 consecutive stimuli (Rossini et al., 1994). Stimulation intensity was set at 120% of the rest motor threshold for all experimental trials. EMG signals were band-pass filtered (50-1000Hz), digitized (2000Hz) and stored on a computer for off-line analysis.

General Procedure. Participants were seated comfortably on a dentist like armchair, their arms stretched out on a arm rest and their hand lying 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 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 (Figure 1A) were of different shape and explicitly of different weight despite 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 10g 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 500g 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 lied pronated on the table, pushing with the fingertips a hidden switch placed at about 20 cm from the object (Figure 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 at random time during the lifting phase of the observed movement, approximately 1.3 sec after movement onset (Figure 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.

Data reduction and analysis. From the EMG data, peak-to-peak amplitudes of the MEPs were determined. Since EMG background activation is known to modulate MEP amplitude (Hess et al., 1987;Devanne et al., 1997), 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 in the remaining trials were removed from the analysis under the following criteria: outliers were considered as values larger than Q3+1.5 x (Q3-Q1) with Q1 the first quartile and Q3 the third quartile computed over the whole set of trials for each subject. Following these three criteria one subject was discarded, due to 80% of bad trials in one of the observation conditions. From the remaining subjects, 13 % of trials were discarded in total.

For each subject, MEP amplitudes recorded for each observation condition were then normalized relative to the subjects' maximal MEP amplitude (measured over all trials and conditions). Subsequently, normalized MEPs were averaged among subjects. RMSe scores of each condition were also normalized relative to the maximal RMSe score (measured over all trials and conditions) and averaged among subjects.

Statistics. Paired T-tests were used to compare peak-to-peak MEP amplitude data recorded during the observation of the heavy and light weight lifting. 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.

RESULTS

During the **observation** of object lifting with a precision grip, individual normalized MEP amplitudes in the FDI muscle revealed a systematic modulation relative to the weight of the lifted object. For six out of seven subjects, MEP amplitude scores were higher during observation of heavy object lifting compared to light object lifting, and this difference was significant in one subject [S3, t=2.395, p=.038] (Figure 2A). At the group level (n=7), this consistent trend led to significantly higher normalized MEP amplitudes for the heavy compared to the light weight observation condition [t=2.8, p=.031] (Figure 2B).

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=.972, p=.369], indicating that experimental results are not likely explained by a modulation in background EMG.

EXPERIMENT 2

Execution and observation of object lifting with a whole hand grip

Experiment 2 was designed to test if the results found in experiment 1 are consistently found during observation of other types of grip, and if the weight-related modulation is specific for the muscles involved in action execution or if it reflects an unspecific activation of the motor system. In addition, in experiment 2, the muscle activation pattern for real execution of lifting different object weights was assessed and compared to the corticomotor responses obtained during the observation of the same lifting actions.

The main differences between the two observational paradigms regard: (i) the observation of a precision grip (Exp 1) or of a whole hand prehension (Exp 2); (ii) the recording of one muscle only (First Dorsal Interosseus) (Exp 1) or of three muscles (Opponens Pollicis, Flexor and Extensor Carpi Radialis) (Exp 2); (iii) the comparison of two weights (Exp 1) or of three weights (Exp 2), and (iv) the involvement of a real agent performing the movement (Exp 1) or the use of videos (Exp 2). Although both types of stimuli (i.e., real actions or video-taped actions) are known to induce a reactivation of primary motor cortex, it may be worth mentioning that reactivations were shown to be more salient for observing real actions compared to video-taped actions (Jarvelainen et al., 2001).

MATERIALS & METHODS

Execution

Task. Five subjects (age range 23-30; 3 females, 2 males) 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 (Figure 3).

EMG. During execution, EMG was simultaneously recorded from the right Opponens Pollicis (OP) muscle and Flexor (FCR) and Extensor Carpi Radialis (ECR) muscles.

Data analysis. Each subject performed the three actions 15 times. In 12 additional trials, the EMG was recorded during maximal voluntary contraction (MVC) of each muscle. EMG-changes (amplitudes) were calculated for a short time-interval of 40 ms during the lifting of the bottle (Figure 3). EMG changes were expressed as the percentage of subjects' muscle-specific MVC-scores.

Observation

Subjects. Twelve subjects (3 males and 9 females) with an age range of 21-35 (mean: 23) participated after providing informed consent. The subjects participating in the action observation experiment were not the same subjects that participated in the action execution experiment.

Electromyographic recordings and TMS. EMG and TMS procedures were similar to those described in Experiment 1. However, MEPs were evoked and measured from the right Opponens Pollicis (OP) muscle and Flexor (FCR) and Extensor (ECR) Carpi Radialis muscles. Although stimulation settings were prioritised for the OP muscle, 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 MH 1990). For all experimental trials, stimulation intensity was set at 130% of the rest motor threshold of the OP muscle. 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. 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 per seconds). 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 (Figure 3). 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 (Figure 3). 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 seconds. Each of the 4 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 (Figure 3). 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.

Data reduction and analysis. The same procedures as in Experiment 1 were adopted for data analysis. Following this procedure, only 4% of all trials (of all subjects) were discarded from further analyses for each muscle (OP-FCR-ECR).

Statistics. MEP Amplitude data recorded during the observation of the three 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.

RESULTS

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 to the FCR muscle (normalized EMG muscle activity recorded from the OP and FCR are visualized in Figure 4A). This was revealed by the two-way ANOVA interaction between 'Muscle' (OP, FCR, ECR) and 'Grip Force' (Empty, Half Full, Full) [F(4,16)=3.22, p<.05]. Main effects of 'Muscle' [F(2,8)=4.91, p<.05] and 'Grip force' [F(2,8)=55.68, p<.001] were also found. Post-hoc analysis of the two-way interaction revealed that for the OP and ECR, all force levels were significantly different from one another, and that modulations in grip force - related to the weight of the lifted object - were more pronounced in the OP and ECR muscle, compared to the FCR muscle (see Figure 4A).

During the **observation** of object lifting, normalized MEP amplitudes were shown to modulate systematically with the force requirements of the action. Moreover, force-related modulations in MEP responses were exclusively found for muscles involved in the execution of the observed action. This was revealed by the two-way ANOVA interaction between ‘Muscle’ (OP, FCR, ECR) and ‘Grip Force’ (Empty, Half Full, Full) [F(4,44)=3.46, p<.05]. A main effect of ‘Muscle’ [F(2,22)=3.81, p<.05], but not of ‘Grip force’ [F(2,22)=2.37, p=.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 to observing the empty bottle [both, p<.01] (Figure 4B). MEP scores yielded from the ECR muscle showed a similar modulation (Empty: 0.48 ± 0.02; Half full: 0.51 ± 0.03; Full: 0.53 ± 0.02) [Empty versus Half full, p=.05; Empty versus Full, p=.007]. In the FCR, on the other hand, no differences in MEP scores were measured for observing the different weight lifting [p>.2] (Figure 4B).

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>.21], which indicated that the MEP amplitude scores were not confounded by modulations in background EMG.

GENERAL 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, corticomotor modulation during action observation is 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 corticomotor excitability was found for the heavy object conditions than for the light object conditions.

Perception of object lifting activates the human motor 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, Exp 1 showed a '*precision grip*' (i.e., opposing the tips of the thumb and index finger), whereas Exp 2 showed a '*whole hand grip*' (i.e., using the thumb and hand palm). Consequently, the type of the 'to be grasped objects' also differed, particularly with respect to the weight ranging from 0 to 500g in Exp 1, and from 0 over 1000 to 2000g in Exp 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 requirements of the observed lifting actions. 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 on the properties of this system by showing that the level of grip force is represented in the observer's motor system. Thus, observation-to-execution mapping includes also some dynamical features of motor control, such as grip force.

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), whereas the actual fine-tuning of grip force has been shown to rely strongly on primary motor cortex 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 (2006) demonstrated that perceptual weight judgements depends 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 functional magnetic resonance imaging (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. However 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 plays 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., 2009b). Therefore, in relation to the studies cited above, we suggest that, in the present experiment, IFG might be occupied with representing 'motor prototypes' (such as the type of grip), whereas M1 is 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, in the present experiments, the force-related modulation in M1 might also have been triggered by 'object-related' cues, such as the filling degree of the bottle in experiment 2, or the type of material in experiment 1. Indeed, the weight of an object, and consequently the grip force needed to lift it, can quite accurately be estimated based on prior knowledge on characteristics of objects (Johansson 1998). In this context, a series of fMRI studies by Grafton & Hamilton identified the parietal region of the mirror neuron system, namely the IPS, to be a key area in representing different target objects during action observation (Hamilton & Grafton, 2006; Grafton & Hamilton, 2007). However, the observation of different object weights alone appeared to be inefficient in triggering force-related modulations in M1 (Leuven group, preliminary TMS work), suggesting that 'the action upon the object' is necessary to elicit weight/force-related responses in M1. 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.

Nonetheless, our data convincingly showed that the motor system is recruited during observed object lifting and that its activity reflects a muscle specific force-related modulation. The potential role of M1 in representing the muscle- and force-related aspects of the observed movement has some functional significance that will be discussed in the following part.

Functional significance of force-related activity 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 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 hypothesise that the reported force-dependent modulations of M1 activity may be functionally relevant for inferring (‘understanding’) the grip force that is produced in the observed lifting actions (which in turn may contribute to the subjects’ ability to estimate the weight of the lifted object). Unfortunately however, no formal assessment of the individual subjects’ ability to judge the produced grip force was obtained such that no firm conclusions can be drawn on this point.

Aside its functional relevance in action understanding, the finding of force-related M1 activations may reveal further insights on *how accurate* force requirements are mapped within the observer’s motor system. From the execution experiment (exp. 2) it was shown that the muscle activity in the OP and ECR muscle was substantially higher for lifting a full compared to lifting a half full bottle. However, the elicited corticomotor 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 weights range of 50 – 850g (increasing with steps of 200g) (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 judging the highest weights (850 g). As such it can be tentatively hypothesised 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 which develop relatively ‘weak’ maximal contractions (such as distal hand muscles involved in fine-grip force tuning) and muscles developing considerably ‘stronger’ maximal contractions (such as proximal arm muscles involved in whole body lifting actions). Nevertheless, future studies should be conducted to specifically address this hypothesis.

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 primary motor cortex 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.

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FIGURE LEGENDS

Figure 1.

Experimental stimuli of experiment 1.

A. Picture of the two objects grasped and lifted in front of the subject. The 500g “Heavy” object (left) was a typical brass balance weight. The 10g “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 during 1s. A TMS pulse was delivered during the lifting phase. 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.

Figure 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.

Figure 3.

Results of experiment 1

A. Individual mean MEP traces for the “Heavy” (black) and “Light” (grey) experimental conditions. Asterisks indicate significant differences ($p<0.05$).

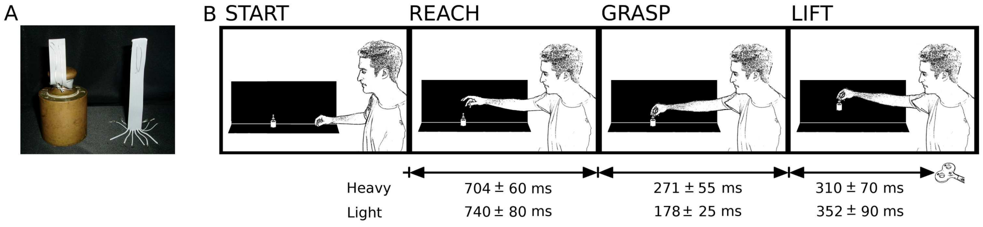
B. Averaged values ($n = 7$) of peak to peak amplitude MEPs recorded during observation of lifting the “Heavy” and the “Light” object. Whiskers indicate standard errors. Asterisks indicate significant differences ($p<.05$). Vertical bars denote ± standard errors.

Figure 4.

Results of experiment 2.

A. Averaged values (n = 5) of muscle activity (EMG) recorded during the **execution** of object lifting with a whole hand grip (expressed as a percentage of the subjects' maximal voluntary contraction (MVC)).

B. Averaged values (n = 12) of peak to peak amplitude MEPs recorded during the **observation** of 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. MEPs evoked from the OP and FCR muscle are presented. Whiskers indicate standard errors. Asterisks indicate significant differences ***p<.001 **p<.01; *p<.05. Vertical bars denote ± standard errors.



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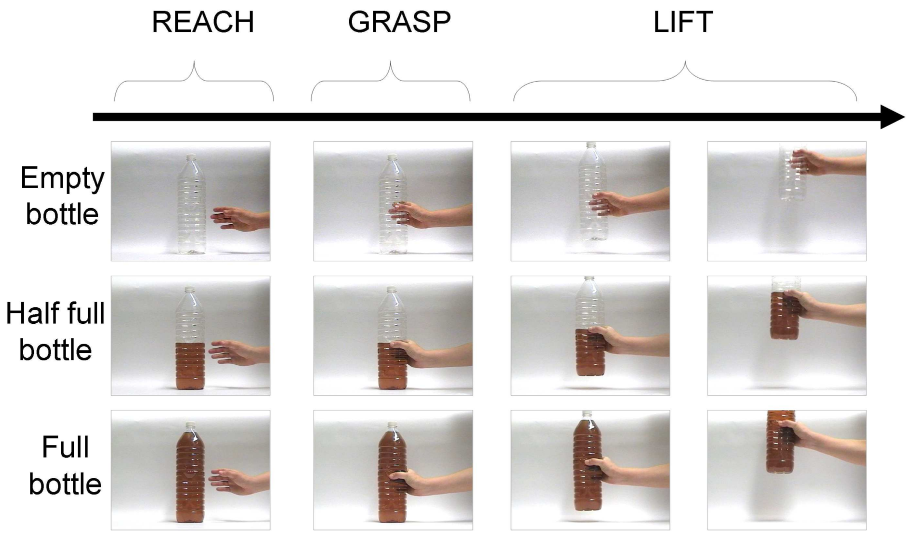

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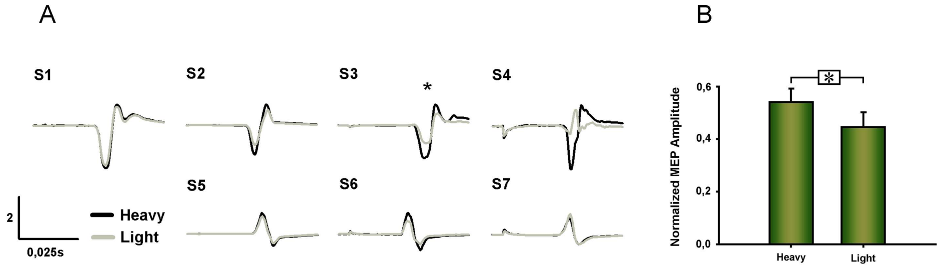
639x399mm (122 x 122 DPI)



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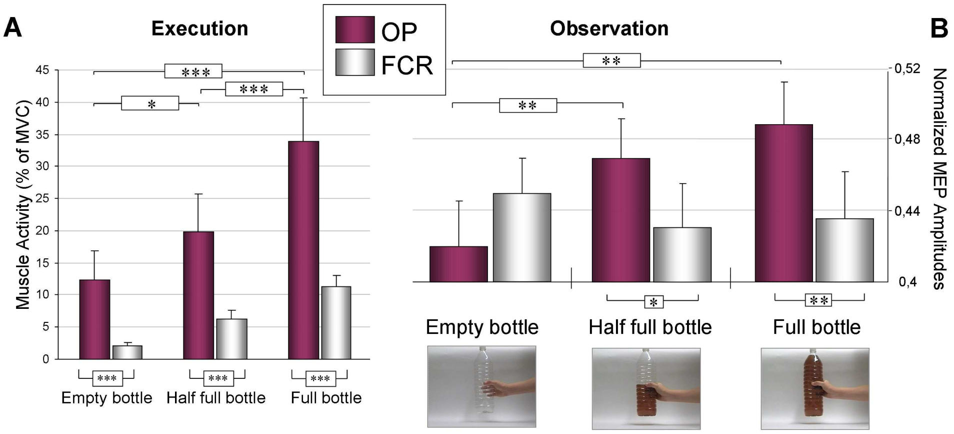
975x296mm (80 x 80 DPI)



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951x449mm (82 x 82 DPI)