

Observing how others lift light or heavy objects: Which visual cues mediate the encoding of muscular force in the primary motor cortex?

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ABSTRACT

Observers are able to judge quite accurately the weights lifted by others. Only recently, neuroscience has focused on the role of the motor system to accomplish this task. In this respect, a previous transcranial magnetic stimulation (TMS) study showed that the muscular force requirements of an observed action are encoded by the primary motor cortex (M1).

Overall, three distinct visual sources may provide information on the applied force of an observed lifting action, namely, (i) the perceived kinematics, (ii) the hand contraction state and finally (iii) intrinsic object properties. The principal aim of the present study was to disentangle these three visual sources and to explore their importance in mediating the encoding of muscular force requirements in the observer's motor system. A series of experiments are reported in which TMS was used to measure 'force-related' responses from the hand representation in left M1 while subjects observed distinct action-stimuli.

Overall, results indicated that observation-induced activity in M1 reflects the level of observed force when kinematic cues of the lift (exp. 1) or cues on the hand contraction state (exp. 2) are available. Moreover, when kinematic cues and intrinsic object properties provide distinct information on the force requirements of an observed lifting action, results from experiment 3 indicated a strong preference for the use of kinematic features in mapping the force requirements of the observed action. In general, these findings support the hypothesis that the primary motor cortex contributes to action observation by mapping the muscle-related features of observed actions.

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1. Introduction

In social interactions, humans demonstrate the remarkable ability to understand and interpret the behaviour of other people in a seemingly effortless way. This ability is proposed to be mediated by the 'mirror neuron system' which was first identified and characterized in frontal and parietal areas of the monkey brain (Rizzolatti & Craighero, 2004). These areas contain 'mirror neurons' that discharge both when the monkey executes hand actions itself and when it observes the same action made by another monkey or the experimenter (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Using movement observation paradigms, functional imaging studies have revealed that analogue fronto-parietal circuits are activated in humans (Buccino et al., 2001; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grezes, Armony, Rowe, & Passingham, 2003). Moreover, when transcranial magnetic stimulation (TMS) is applied during the mere observation of actions, the primary motor cortex (M1) becomes increasingly activated in a strictly time-locked and

muscle specific way (Borroni, Montagna, Cerri, & Baldissera, 2005; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Gangitano, Mottaghy, & Pascual-Leone, 2001).

In the past, a number of TMS studies have been conducted to characterize and describe the process of observation-to-execution mappings within the motor system (for a review on TMS studies: Fadiga, Craighero, & Olivier, 2005). In this respect, a recent TMS study convincingly demonstrated that the force requirements of an observed action are represented in the observer's M1: corticomotor excitability of the thumb muscle was shown to be significantly higher when observing the grasping and lifting of a heavy as compared to a light object (Alaerts et al., 2010). No such force-related modulation was measured in muscles not involved in the grasp and lift movement. As such, the motor system of an observer appears to encode the observed force requirements needed to lift particular objects. However, from this previous study, it remains largely unknown which specific visual features of the observed lifting actions were important to mediate the encoding of grip force requirements, as in the adopted experimental video clips, distinct visual features – potentially providing information about the applied force (see below) – were presented simultaneously. The principal aim of the present study was therefore to disentangle

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gle these distinct visual features and to characterize their relative contribution in mediating force-encoding within the observer's motor system. Overall, three types of visual features can be distinguished that may contribute to a person's ability to infer the applied force from observing the grasping and lifting of a bottle: A first important cue is the perceived *kinematic pattern* by which the bottle is grasped and lifted (Bingham, 1987; Grezes, Frith, & Passingham, 2004; Hamilton, Joyce, Flanagan, Frith, & Wolpert, 2007a; Shim & Carlton, 1997). For example, if the bottle is heavy, the durations of the grasp- and lift-phase will be longer, than for lifting a lighter bottle. Second, the *hand contraction state*, such as observable differences in tension/pressure produced in the acting hand and fingers (i.e., whitening and stretching of the skin during high force production), may provide additional information on the level of exerted force in a grasp/lift action. Finally, another reliable cue refers to features of the bottle itself, such as its size, filling degree or the type of material (e.g. plastic versus glass). These *intrinsic object properties* are usually acquired through experience, such that one would predict large objects to be heavier than small objects or that a filled bottle is heavier than an empty one (Cole, 2008; Flanagan & Beltzner, 2000; Forssberg et al., 1992; Gordon, Forssberg, Johansson, Eliasson, & Westling, 1992; Gordon, Westling, Cole, & Johansson, 1993; Johansson & Westling, 1988).

Here, we aimed to explore the relative contribution of (i) overall kinematics, (ii) hand contraction state and (iii) intrinsic object properties in mediating the encoding of muscular force requirements in the observer's motor system. For this purpose three separate TMS experiments were conducted in which corticomotor excitability was measured from the hand and forearm representations in M1 during the passive observation of distinct grasp/lift movements.

In **Experiment 1**, two video clips showed the grasping and lifting of either light or heavy objects. Across both weight conditions, the objects looked identical and all tension/pressure cues concerning the exerted force (i.e., the hand contraction state) were concealed by covering the actor's hand with a glove and sleeve. As such, the force needed to lift the object could only be inferred from differences in the overall **kinematic motion pattern** of the grasping/lifting action. If kinematic cues alone are sufficient in mediating force-related activity in M1, we expected excitability of M1 to be higher in the heavy than in the light object observation condition.

In **Experiment 2**, we aimed to explore whether the presentation of pressure/tension cues on exerted grip force (such as differences in skin colour and stretch) is sufficient to mediate the encoding of force requirements in the observer's motor system. To do so, two video clips were created in which an actor's hand grasped objects with identical appearance while exerting either no, or maximal isometric force on them. The object was never lifted or moved from its initial position (i.e., isometric contraction induces no shortening of the muscles, hence no obvious movement) such that only differences in the **hand contraction state** were available to infer the exerted grip force in the acting hand. If cues from the hand contraction state alone are sufficient to mediate force-related activity in M1, we expected excitability of M1 to be higher for observing maximal isometric force production, compared to no force production.

Finally, in **Experiment 3**, the relative importance of object versus kinematic cues in mediating force-related activity in M1 during observed object lifting was tested in the following way: Four objects were created which differed from each other with respect to their weight (light or heavy) and/or filling level (low filling or high filling). In two, the weight of the object corresponded to its filling degree, i.e., (i) high filling/heavy and (ii) low filling/light, whereas in the other two, the actual weight of the box did not correspond to its filling degree, i.e., (iii) high filling/light and (iv) low filling/heavy. Since the kinematic trajectory of lifting these objects corresponds to the actual weight of the object, this design enabled us to disentangle

the influence of object versus kinematic cues on force-encoding in the following way: If **intrinsic object properties** are predominant in mediating force-related activity in M1, we expected M1 excitability to be higher for observing the lifting of full as compared to relatively empty objects, irrespective of their actual weights. However, if **kinematic cues** are predominant, we expected M1 excitability to be modulated mainly in accordance to the actual weight of the object.

2. Methods

2.1. Subjects

Fifteen subjects participated in Experiment 1 (6 males, 9 females, mean age 24), 16 in Experiment 2 (6 males, 10 females, mean age 25) and 22 participated in Experiment 3 (12 males, 10 females, mean age 23). Fifteen participants of Experiment 1 also participated in Experiment 2. Importantly, in half of these subjects the experimental session started with Experiment 1, whereas in the other half, the experimental session started with Experiment 2. All participants were right-handed, as assessed with the Edinburgh Handedness Questionnaire (Oldfield, 1971) and were naive about the purpose of the experiment. Written informed consent was obtained before the experiment and all subjects were screened for potential risk of adverse effects during TMS. The experimental procedure was approved by the local Ethics Committee for Biomedical Research at KU Leuven and conformed with The Code of Ethics of the World Medical Association (Declaration of Helsinki) (Rickham, 1964).

2.2. Electromyographic recordings and TMS

Surface electromyography (EMG) was performed with Ag-AgCl electrodes (Blue Sensor SP) placed over the muscle belly and aligned with the longitudinal axis of the muscle. EMG activity was recorded simultaneously from the right Opponens Pollicis (OP) thumb muscle and wrist Flexor (FCR) and Extensor (ECR) Carpi Radialis muscles. Both the OP and ECR muscle were shown to be actively involved in the grasping and/or lifting actions of the presented video's, whereas the FCR is much less involved (Alaerts et al., 2010, and unpublished observations). Focal transcranial magnetic stimulation (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. The optimal scalp position was defined as the position from which Motor Evoked Potentials (MEPs) with maximal amplitude were recorded in the right OP muscle. The rest motor threshold (rMT) was defined as the lowest stimulus intensity evoking MEPs in the OP with an amplitude of at least 50 μ V in 5 out of 10 consecutive stimuli (Rossini et al., 1994). Subjects' rest Motor thresholds, expressed as a percentage of the maximum stimulator output, varied from 33% to 58% in *Experiment 1* (mean 44%), from 33% to 53% in *Experiment 2* (mean 43%), and from 33% to 53% in *Experiment 3* (mean 41%). For all experimental trials, stimulation intensity was set at 130% of the subjects' rMT. Parameter setting procedures were prioritised for the OP muscle but MEPs were simultaneously obtained for the FCR and ECR muscles. FCR and ECR stimulation parameters were assumed to be satisfactorily similar, due to the overlapping representations of finger and forearm flexor and extensor muscles (Schieber, 1990). EMG recordings 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.

2.3. 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. Before each experiment, video clips were presented to the subjects to familiarize them with the experimental stimuli. Importantly however, no explicit information was provided on the type of video presented (i.e., the observing subjects had no prior knowledge on the weight of the lifted objects in the video's of experiments 1 and 3). 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. Vision of their own hand and forearm was never allowed. Muscle relaxation was monitored, and, whenever EMG activity became apparent during data collection, the trial was discarded and repeated. In all experiments, stimuli consisted of different video clips presenting object grasping and/or lifting. During the presentation of each video clip, a single TMS pulse was delivered at a slightly randomized time point during the object manipulation phase (lifting in experiments 1 and 3 and grasping in experiment 2). Video presentation was controlled by Blaxton Video Capture software (South Yorkshire, UK). Signal Software (2.02 Version, Cambridge Electronic Design, UK) was used to synchronize video presentation and TMS triggering.

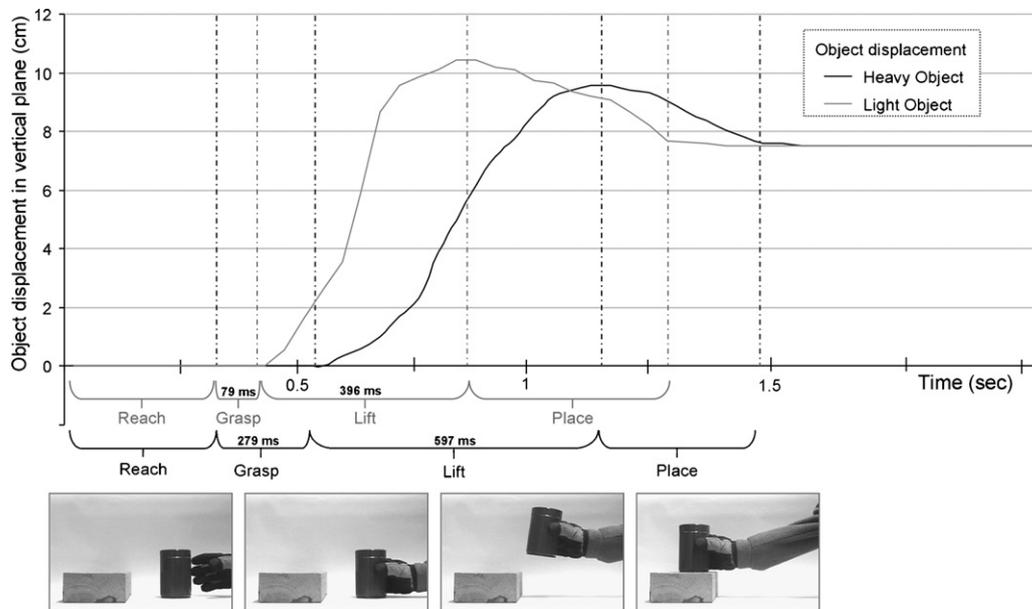


Fig. 1. Kinematic trajectories measured from the two video clips of experiment 1. The kinematic trajectory is divided into four distinct phases, namely, the reach, the grasp, the lift, and the place phase. *Reach* was defined as the time from the start of the movement until the point of hand-object contact. *Grasp* lasted from the end of reach until the start of object displacement. *Lift* lasted from the start of object motion to the object's peak height, and *place* from peak height until the end of object displacement as the object was put on the shelf. Grasp and lift duration differed considerably between heavy (black line) and light (grey line) object lifting. The averaged velocity in the vertical plane during the lift phase was respectively 0.021 cm/ms and 0.014 cm/ms for light and heavy object lifting (slope of the curve).

2.4. Stimuli

Experiment 1. Stimuli consisted of two video clips presenting grasping and lifting of objects with identical appearance, but with different weights, respectively, 0.1 kg (Light object) and 2.1 kg (Heavy object). In both clips, the right hand of an actor reached for the object, grasped it with a whole hand grip and lifted it to place it on an elevated platform (reach-grasp-lift-place) (Fig. 1). To conceal any muscle- or skin-related cues concerning the exerted force, the actor's hand was covered with a glove and sleeve. Thus, the only visible difference between the two conditions was the kinematic profile of the trajectories shown in the video. MTrackJ software (Biomedical Imaging Group, Rotterdam, NL) was used to quantify the trajectories of the lifted objects as shown in the two video clips on a frame-by-frame basis. MTrackJ is an ImageJ plugin (National Institutes of Health, Maryland, US) designed for manual tracking of moving objects in image sequences. The kinematic motion trajectory can be divided into 4 distinct phases, namely, the reach, the grasp, the lift, and the place phase (Fig. 1). *Reach* was defined as the time from the start of the movement until the point of hand-object contact. *Grasp* lasted from the end of reach until the start of object displacement. *Lift* lasted from the start of object motion to the object's peak height, and *place* from peak height until the end of object displacement as the object was put on the shelf. The actor in the video had no prior knowledge on the weight of the to-be-lifted object, such that spontaneous 'typical' lifting actions were obtained. Overall, Fig. 1 showed that the grasp and lift duration differed considerably between heavy and light object lifting, whereas differences in duration were small for the reach and place phase. Vertical velocity was calculated from the position data derived from the frame-by-frame analysis of the video and smoothed by a 5-point sliding average. The averaged vertical velocity, calculated for the successive frames of the lifting phase, was respectively 0.021 cm/ms and 0.014 cm/ms for light and heavy object lifting.

The two video clips were 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 pseudo-random time point during the object lifting phase. For each video, TMS stimulation timing corresponded to the time interval at which the vertical displacement of the lifted object reached 6–8 cm (see Fig. 1). As such, 20 MEPs were recorded for each condition and subject, resulting in 40 MEPs in total. An informal debriefing was performed after the experimental session to assess whether subjects perceived differences between the two observation conditions.

Experiment 2. Stimuli consisted of two video clips presenting the manipulation of objects with identical appearance. In each video clip, the right hand of an actor entered the scene from the right side and grasped the object without moving it for a duration of approximately eight seconds. During the grasping phase, either (i) no force (Low), or (ii) maximal isometric force (High) [app. 60 N] was exerted on the object (Fig. 4). Importantly, the object was never lifted or moved from its initial position at any time. Thus, differences in muscular force were only expressed in terms of the tension/pressure produced by the acting hand and fingers; differences in the skin colour and form of the thumb were the most reliable visual features conveying

the force requirements. No kinematic cues or other features (such as tremor) were visible. All video clips were presented 10 times in blocks of four, with the block presentation order randomized within and across subjects. During the presentation of each video clip, two single TMS pulses were delivered at a pseudo-random time point during the object holding phase (inter-stimulus interval of approximately 4–5 s). As such, 20 MEPs were recorded for each condition and subject, resulting in 40 MEPs in total. An informal debriefing was performed after the experimental session to assess whether subjects perceived differences between the two observation conditions.

Experiment 3. Stimuli consisted of four video clips presenting grasping and lifting movements of different transparent objects. In all clips, the right hand of an actor reached for the object, grasped it with whole hand grip and lifted it to place it on a small platform (Fig. 2). The actor in the video had no prior knowledge on the weight of the to-be-lifted object, such that spontaneous 'typical' lifting actions were obtained. Four different objects (i.e., transparent boxes filled with raisins) were created which differed with respect to their weight (light = 0.5 kg or heavy = 1.2 kg) and with respect to their filling level (low filling = 35% filled, or high filling = 80% filled). In two, the weight of the object corresponded to its filling degree, i.e., (i) high filling, heavy weight (1.2 kg), and (ii) low filling, light weight (0.5 kg). In the other two, the actual weight of the box did not correspond to its filling degree, i.e., (iii) high filling, light weight (0.5 kg), and (iv) low filling, heavy weight (Fig. 2). To create the 'incongruent objects', raisins (in the inner part of the box) were replaced by either styrofoam (to decrease weight of the 'high filling, light weight' object) or by metal (to increase weight of the 'low filling, heavy weight' object). As shown in Fig. 2, the kinematic trajectory differed between light and heavy objects (grey versus black), but not between 'low filling' and 'high filling' objects (solid lines versus dotted lines).

The four video clips were 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 object lifting phase. For each video, TMS stimulation timing corresponded to the time interval at which the vertical displacement of the lifted object reached 18–20 cm (see Fig. 2). In order to measure 'spontaneous' (unbiased) M1 responses to the observed video clips and to avoid the potential use of cognitive strategies, we chose not to ask subjects concerning their subjective perception of the presented video clips after the trial.

2.5. Data analysis

From the EMG data, peak-to-peak amplitudes of the MEPs were determined. Since background EMG is known to modulate the MEP amplitude (Devanne, Lavoie, & Capaday, 1997; Hess, Mills, & Murray, 1987), pre-stimulation EMG was assessed in all three experiments by calculating the root-mean-square error scores (RMSE) across a 50 ms interval prior to TMS stimulation. For each subject and for each muscle separately, mean and standard deviation of the background EMG scores were computed over all trials. Trials with background EMG deviating from the mean by more than 2.5 standard deviation, were removed from further analysis. Finally, extreme peak-to-peak amplitudes values were considered as outliers and removed from the

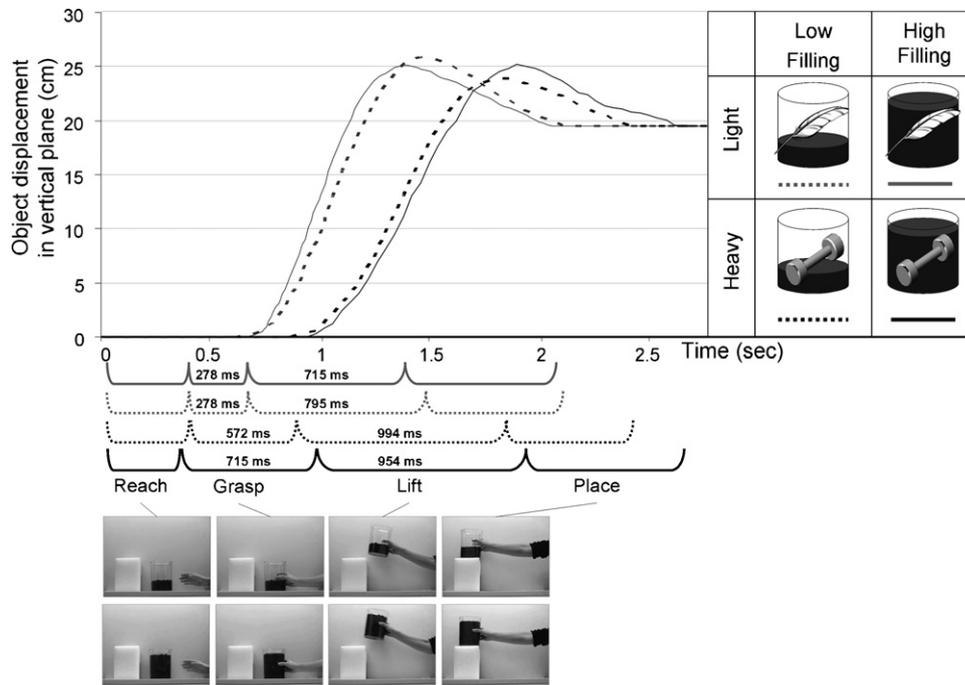


Fig. 2. Kinematic trajectories measured from the four video clips of experiment 3. The kinematic trajectory is divided into four distinct phases, namely, the reach, the grasp, the lift, and the place phase. *Reach* was defined as the time from the start of the movement until the point of hand-object contact. *Grasp* lasted from the end of reach until the start of object displacement. *Lift* lasted from the start of object motion to the object’s peak height, and *place* from peak height until the end of object displacement as the object was put on the shelf. Grasp and lift duration differed substantially between heavy and light object lifting. The averaged velocity in the vertical plane during the lift phase was approximately 0.03 cm/ms and 0.02 cm/ms for respectively light and heavy object lifting (slope of the curve). It can be seen that the kinematic trajectory corresponded to the actual weight of the box, which was either congruent, or incongruent to the object-related cue (i.e. the filling degree).

analysis when they exceeded $Q3 + 1.5 \times (Q3 - Q1)$ with $Q1$ the first quartile and $Q3$ the third quartile computed over the whole set of trials for each subject (Electronic Statistics Textbook, 2007, StatSoft, Inc. Tulsa). Following these criteria, only 3% (54 out of 1800) of all trials were discarded from the analyses in *experiment 1*, 3% in *experiment 2* (112 out of 2280), and 4% in *experiment 3* (198 out of 5280).

Subsequently, MEPs were normalized relative to the subjects’ maximal MEP amplitude (which was computed from all remaining trials) (MEP/MEP_{MAX}). To analyse modulations in background EMG across observation conditions, RMSE scores were normalized accordingly ($RMSE/RMSE_{MAX}$).

2.6. Statistics

Statistics were calculated with Statistica 7.0 (StatSoft, Inc. Tulsa, USA). The level of significance was set to $\alpha = 0.05$. For each muscle, MEP peak-to-peak amplitude data were subjected to analyses of variance (ANOVA).

To address whether peak-to-peak MEP amplitude scores were confounded by modulations in background muscle activity, the background EMG data (normalized RMSE-scores) were subjected to analogous statistical analyses as the MEP data.

3. Results

3.1. Experiment 1

3.1.1. MEP amplitudes

Observation of the kinematics associated with lifting a heavy object triggered substantially higher MEP responses in the OP and ECR muscles than observing the kinematics associated with lifting a light object (Fig. 3). No such effect was found in the FCR muscle. These findings are supported by a one-way ANOVA for the within factor ‘Object weight’ (Light, Heavy) which revealed significance for the OP [$F(1,14) = 17.88, p < .01$] and ECR muscle [$F(1,14) = 5.76, p < .05$], but not for the FCR muscle [$F(1,14) = .18, p = .676$].

3.1.2. Background EMG

The background EMG was generally small and condition-specific modulations were minimal. This was tested by conducting a similar one-way ANOVA analysis to the corresponding background

EMG data (normalized RMSE-scores). Here, the effect of ‘Weight’ did not reach significance [$F < 1.48, p > .244$] which indicates that the MEP amplitude scores were not confounded by modulations in background EMG.

3.2. Experiment 2

3.2.1. MEP amplitudes

Observation of strong isometric contraction yielded substantially higher MEP responses in the OP and ECR muscles compared to

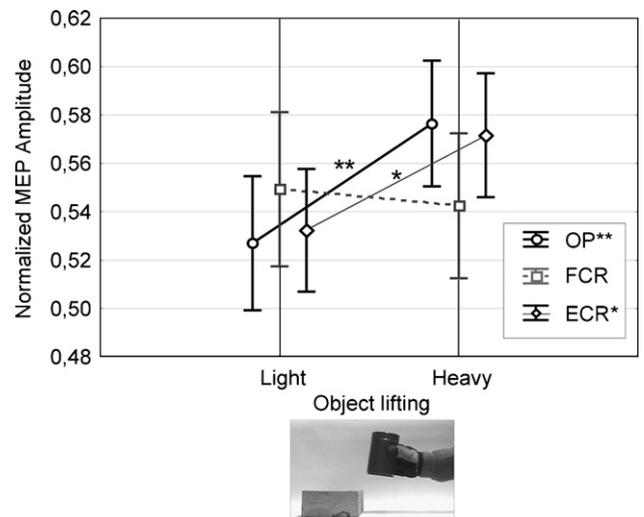


Fig. 3. Experiment 1: Normalized Peak-to-peak MEP Amplitudes recorded from the OP, FCR and ECR muscles, during the observation of light and heavy weight lifting. Vertical bars denote \pm standard error. Significant differences between conditions are indicated [$*p < .05$; $**p < .01$].

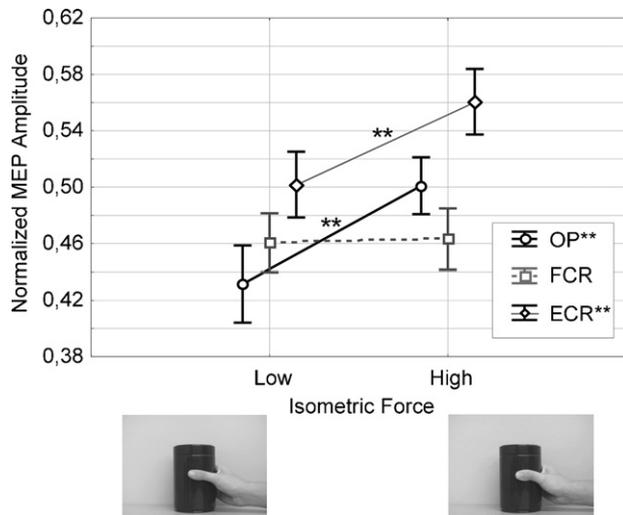


Fig. 4. Experiment 2: Normalized Peak-to-peak MEP Amplitudes recorded from the OP, FCR and ECR muscles, during the observation of low and high isometric contraction exerted on a tin can. Vertical bars denote \pm standard error. Significant differences between conditions are indicated [$**p < .01$].

the observation of low isometric contraction (Fig. 4). No such effect was found for the FCR muscle. These findings are confirmed by the ANOVA for the within factor 'Isometric force' (Low, High), which revealed a significant effect for the OP [$F(1,15) = 12.41, p < .01$] and ECR muscle [$F(1,15) = 10.69, p < .01$], but not for the FCR muscle [$F(1,15) = .045, p = .834$]. Although any intrinsic object features were lacking and kinematic cues were minimal in the observed video clip, perception of the hand contraction state was apparently sufficient to trigger the encoding of force requirements in a highly muscle specific way.

3.2.2. Background EMG

The one-way ANOVA analysis conducted on the background EMG data, did not reveal an effect of 'Isometric force' [$F < .189, p > .67$], which indicates that the MEP amplitude scores were not confounded by modulations in background EMG.

3.3. Experiment 3

3.3.1. MEP amplitudes

MEP responses from the OP muscle were modulated according to the weight but not to the filling level of the object (Fig. 5). MEP

amplitudes were subjected to repeated measures ANOVAs with the within factors 'Weight' (Light, Heavy) and 'Filling degree' ('Low filling', 'High filling'). Corticomotor excitability was significantly lower when observing the light versus heavy object conditions, as indicated by a main effect of 'Weight' [$F(1,21) = 6.46, p < .05$]. By contrast, the intrinsic object characteristics appeared to have no substantial effect such that neither the main effect of 'Filling degree' nor the interaction reached significance [$F(1,21) = .678, p = .419$; $F(1,21) = .071, p = .793$]. For the FCR and ECR muscles, none of the main or interaction effects reached significance [all, $F(1,21) < 2.8, p > .1$]. However, MEP responses from the ECR muscle did show a tendency similar to the modulation found in the OP muscle [$F(1,21) = 2.1, p = .15$] (Fig. 5). In addition, for the FCR muscle, a tendency was revealed towards slightly higher MEP responses when the lifting of objects with a high filling degree was observed [$F(1,21) = 2.8, p = .11$].

3.3.2. Background EMG

No modulations in background EMG were found [$F < 2.173, p > .155$].

4. Discussion

In the present study, we aimed to investigate which visual cues mediate the encoding of force requirements of observed grasping and lifting actions in the observer's M1. We investigated three distinct visual sources which may provide information on the applied force of an observed lifting action, namely, (i) the perceived kinematics, (ii) the hand contraction state and finally (iii) intrinsic object properties. This study revealed 3 novel findings: In experiment 1, it was shown that perceiving the kinematic trajectory, associated with lifting heavy or light weight objects, was sufficient to induce force-related activity modulations in the observer's primary motor cortex (M1). In experiment 2, we showed that the observation of isometric contraction (no muscle shortening, hence no obvious movement) produced an increase in corticomotor activity of M1. As such, the sole presentation of pressure/tension cues on exerted muscular force (i.e., the hand contraction state) appeared to be sufficient to trigger force-related activity within the observer's motor system. Finally, when both kinematic and object cues provided distinct information on the force requirements of an observed lifting action, results from experiment 3 indicated a strong preference for the use of kinematic motion features in mapping the force requirements of observed object lifting (i.e., higher corticomotor activity in M1 for observing the kinematic trajectory, associated with lift-

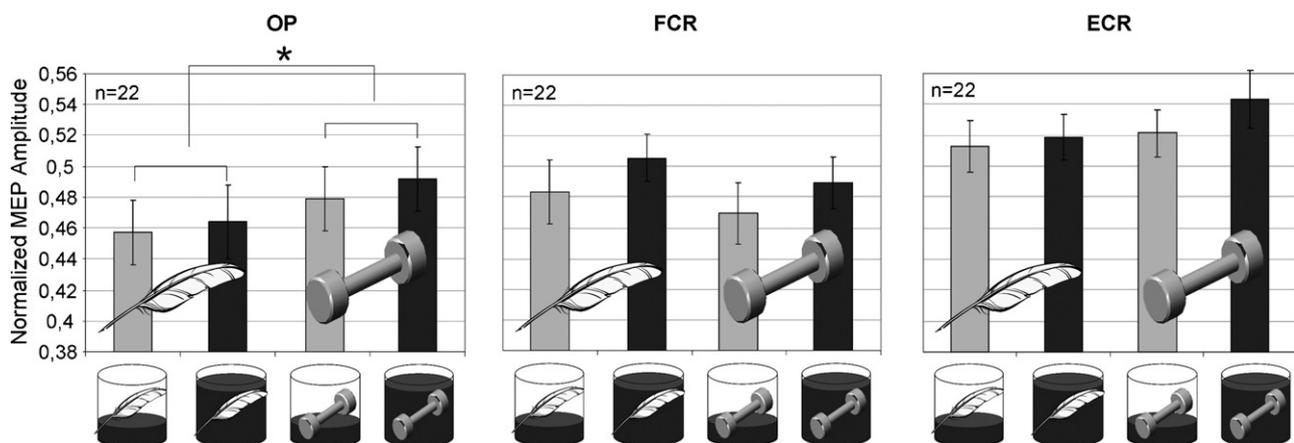


Fig. 5. Experiment 3: Normalized MEP amplitudes (group means, $n = 22$) recorded from the OP, FCR and ECR muscles, during the observation of object lifting. Objects were (i) either full (black bars) or relatively empty (grey bars) and (ii) either heavy or light. Vertical bars denote \pm standard error. Significant differences between conditions are indicated [$*p < .05$].

ing heavy objects, compared to observing the kinematic trajectory, associated with lifting light objects). By contrast, effects of intrinsic object characteristics of the lifted object (i.e., its filling degree) on the encoding of force in M1 were virtually negligible.

4.1. Experiments 1 and 3: perceived kinematics mediate force encoding in motor system

Results from Experiment 1 indicated that perceiving the kinematic trajectory – associated with lifting heavy or light objects – was sufficient to mediate force-related activity in the observer's primary motor cortex (M1). Moreover, the force-related modulations in M1 were only found for those muscles that are normally active during the actual performance of the lifting action (i.e., the OP and ECR muscle, but not the FCR muscle, Alaerts et al., 2010).

The importance of kinematic cues in mapping the force-requirements of an observed lifting action was further supported by the results obtained in experiment 3. Here, a strong predominance for the use of kinematic cues over object-related cues was revealed. More specifically, MEP responses were shown to be considerably higher for observing kinematics associated with lifting heavy objects than observing kinematics associated with lifting light objects, and this, irrespective of the intrinsic object characteristics (i.e., the filling degree). It should be noted however, that in experiment 3, this effect was only found robustly in the OP muscle, and not in the ECR (here, only a tendency towards a similar force-related effect was revealed). Overall, this may seem at odds with findings from experiment 1 that revealed a robust force-related effect for both muscles. However, taken into account that the optimal weight discrimination range might be different for muscles that develop relatively 'weak' maximal contractions (such as finger muscles involved in fine force tuning (e.g. the OP)) and muscles developing relatively 'stronger' maximal contractions (such as wrist muscles involved in stabilizing the lift (e.g. the ECR)), it can be hypothesised that the finding of more robust force-related responses of the ECR in experiment 1 (as opposed to experiment 3) relates to the fact that the weight range of the lifted objects was substantially larger in experiment 1 (0.1–2.1 kg), compared to experiment 3 (0.5–1.2).

Overall, data from experiments 1 and 3 confirm previous evidence on an observation-to-execution matching mechanism within motor areas and extend these findings by emphasizing that movement observation is extremely sensitive to movement kinematics. Indirect evidence on the importance of kinematics in motion perception comes from studies on interference between executed and perceived movements. It was demonstrated that interference with movement execution was only found when the simultaneously observed movement was performed with human-like kinematics (Chaminade et al., 2005; Kilner, Paulignan, & Blakemore, 2003; Stanley, Gowen, & Miall, 2007). In addition to the behavioural evidence, a recent fMRI study showed that mirror neuron areas were more strongly activated during the observation of movements obeying the 2/3 power law (which characterises curved human movements) compared to any other type of motion (Dayan et al., 2007). In line with this finding, the data of experiments 1 and 3 indicate that activity modulations within the observer's motor system are highly sensitive to changes in the observed kinematics.

Furthermore, behavioural studies on weight judgement tasks have indicated that the observed kinematics of object lifting can provide important cues to judge the weight of the lifted box (i.e. lift duration: Hamilton et al., 2007a) (form of the lift trajectory: Bingham, 1987) More specifically, results from a series of experiments by Bingham (1987) demonstrated that the form of the lift trajectory can mediate weight perception based on visual cues. Results from a more recent study by Hamilton et al. (2007a) suggested that the duration of the early part of the lift movement

has a strong influence on the observer's judgement of the weight of the lifted box, but that grasp and later phases of lift can also contribute. In the present experiments (1 and 3), measurements of corticomotor excitability were only assessed during the 'late' lifting phase (i.e., a point at which several salient kinematic cues on object weight are revealed). Accordingly, in order to firmly disentangle the relative importance of distinct kinematic cues (i.e., form of lift trajectory, duration of grasp, early and late lift phase) in mediating force-related M1 responses, future experiments, using a similar TMS-paradigm, should be conducted in which corticomotor excitability is assessed at different phases of the kinematic motion trajectory.

4.2. Experiment 2: observing isometric contraction mediates force encoding in motor system

Results from Experiment 2 indicated that the observation of isometric contraction (no muscle shortening, hence no obvious movement) produced an increase in corticomotor activity of M1. As such, the sole presentation of pressure/tension cues on exerted grip force (revealed by differences in skin colour and stretch) appeared to be sufficient to trigger force-related activity within the observer's motor system.

In the past, a number of studies have investigated the relationship between brain activation and force production during isometric contractions. In this context, both imaging studies in humans and animal experiments reported a strong correlation between activity within motor areas and force production (Dai, Liu, Sahgal, Brown, & Yue, 2001; Dettmers et al., 1996a; Dettmers et al., 1996b; Evarts, 1968; Evarts, Fromm, Kroller, & Jennings, 1983). For example, a recent experiment in monkeys showed a linear relation between the activation of muscles (assessed with EMG) and the activity within M1 (Townsend, Paninski, & Lemon, 2006). All together, these data unanimously suggest an important role for M1 in fine-tuning the level of isometric force produced in peripheral muscles. However, it was never investigated so far whether this pattern of M1 activity was also reflected during the mere observation of isometric contractions. Although only two levels of force production (i.e., hardly any force versus maximal isometric contraction) were presented in the present experiment, the data suggest a replication of the linear relationship between observed muscle contraction and activity within primary motor cortex. Further studies, including additional (in-between) levels of force, should verify this assumption. Nevertheless, it appears that observation-to-execution mapping within motor areas is a finely tuned process, even when visual cues on the perceived action are not goal-related and contain only minimal kinematic cues.

4.3. Experiment 3: influence of intrinsic object properties?

Experiment 3 was essentially designed to explore the relative importance of kinematic cues *versus* intrinsic object properties to encode observed force requirements. Consequently, the design was such that measurements of corticomotor excitability were taken only during the 'late' lifting phase, as at this time point, not only object-related cues, but also the most salient kinematic cues on object weight are revealed (Hamilton et al., 2007a). Based on this design, the contribution of intrinsic object properties was compared *relative* to the impact of kinematic cues. Group results indicated that – when both kinematic and object cues provide distinct information on the force requirements of an observed lifting action – the encoding of force in the observer's motor system seems to depend predominantly on cues from the observed kinematic profile.

However, this result does not univocally imply that object properties are totally irrelevant in the context of movement observation.

Previous research indicated that the motor system makes use of internal models of object properties to predict the load forces that will arise when acting on objects (Flanagan, Bowman, & Johansson, 2006). In this respect, the observation that MEP responses from the OP and ECR muscle tended to be either maximal or minimal when *both cues* (i.e., kinematics and filling degree) informed the observer that the object was either heavy or light (Fig. 5), may support the notion that intrinsic object properties can have an additional, albeit far more subtle influence on the encoding of observed force requirements in M1. Also in the FCR muscle (which is much less involved in the observed actions), a slight tendency was revealed toward higher MEP responses when objects with a high filling degree were observed. From this perspective, although highly speculative, it is proposed that the first sight of the 'to be lifted object' in our study may have evoked an a priori prediction of its putative weight (apparently in a non-muscle specific way, hence the object-driven tendency in all three muscles), which however, became updated when the kinematic motion pattern unfolded (i.e., more specific to the actual muscles used in the observed action). Data from a very recent study provide already first indications that motor programs for object grasping can indeed be influenced by some specific intrinsic features of objects (Buccino, Sato, Cattaneo, Rodà, & Riggio, 2009). However, future research is needed to explore these effects further.

Based on the results from experiment 3, we conclude that the actual weight of the lifted object (as revealed by the observed motion kinematics) drives force-related responses in M1 rather than the appearance of the object when both cues are available.

4.4. Functional significance and potential mechanisms underlying force-related activity in M1

The TMS paradigm used in the present study allows us to draw strong inferences only with respect to changes of excitability of the motor cortex. However, it is tempting to speculate on the potential neural mechanisms underlying these changes. Three alternative interpretations can be put forward.

Overall, our results are in good agreement with the **mirror neuron theory** (Fadiga et al., 2005; Rizzolatti & Craighero, 2004) which proposes that mirror neuron regions provide a representation of actions that allows the observer to 'simulate' observed actions in his own motor repertoire, in order to understand or interpret the actions made by others (Rizzolatti, Fogassi, & Gallese, 2001). In this context, the parietal node of the mirror system, namely the inferior parietal lobule (IPL) is assumed to provide a 'goal-description' of the observed action, by defining the identity and function of the to-be-grasped object (Hamilton & Grafton, 2006; Hamilton & Grafton, 2007b; Tunik, Rice, Hamilton, & Grafton, 2007), whereas the frontal part, namely the inferior frontal gyrus (IFG) is suggested to represent the kinematic features of observed actions (Grafton & Hamilton, 2007; Hamilton & Grafton, 2007b; Pobric & Hamilton, 2006). Importantly, via its frontal node (IFG), the parieto-frontal mirror circuit is strongly reciprocally connected to the primary motor area (M1) (Dum & Strick, 2005; Matelli, Camarda, Glickstein, & Rizzolatti, 1986; Shimazu, Maier, Cerri, Kirkwood, & Lemon, 2004), such that observation-induced modulations of M1, as assessed with TMS, are most likely driven by these 'upstream' mirror areas. Indeed, during action execution, the IFG is known to provide a significant input to M1 (Davare, Lemon, & Olivier, 2008; Davare et al., 2009) and a similar 'parallel' IFG-M1 circuit is hypothesised to be recruited during action observation.

From this perspective, the activity modulations measured from M1 in our experiments may reveal interesting insights into the way the presented visual inputs are conveyed throughout the mirror circuit to reach M1. More specifically, experiment 1 showed that changes in the kinematic profile of an observed action yielded a

highly muscle specific pattern of activity in the hand area of M1. Provided that the IFG is occupied with representing these kinematic features, it can be hypothesized that M1 received strong input from this region to translate this information into muscle-related coordinates (i.e., stronger M1 activations for observing kinematic profiles associated with heavy object lifting). Indeed, M1 appeared to reflect quite accurately the force requirements of the observed actions both in terms of muscle type, and the level of force they produce. This is remarkable, since force requirements were only indicated indirectly from the observation conditions of experiment 1 (i.e., only kinematic trajectories were displayed). As such, this finding indicates that the motor system of the observer resonated with the perceived actions "as a whole" and represented also those aspects that were not explicitly shown. Debriefing indicated that all subjects perceived one object to be heavier than the other based on the observed kinematics. As such, in line with the mirror neuron hypothesis, we tentatively suggest that the activity modulations in M1 might have contributed, at least partly, to the subjects' ability to infer object weight, i.e., by mapping the force-requirements of the observed action in a muscle-centred coordinate frame within M1. This notion is supported by a recent study suggesting a prominent role for the motor system in predicting the outcome of observed actions by reading body kinematics (Aglioti, Cesari, Romani, & Urgesi, 2008). Moreover, the hypothesis of a more prominent role of M1 in the process of motor simulation has been suggested before (Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Alaerts, Swinnen, & Wenderoth, 2009; Kilner & Frith, 2007; Lepage, Lortie, & Champoux, 2008; Pineda, 2008) and is in line with the recent discovery of M1 neurons with mirror properties in the monkeys brain (Tkach, Reimer, & Hatsopoulos, 2007).

Even though our data are in good agreement with the current mirror neuron theory, an alternative, not mutually exclusive interpretation can be that the experimental context activated movement representations in terms of stored **internal models** (Bursztyn, Ganesh, Imamizu, Kawato, & Flanagan, 2006; Jenmalm, Schmitz, Forssberg, & Ehrsson, 2006). More specifically, experiment 2 showed that the presentation of tension/pressure cues on grip force was sufficient to mediate force-related activity within the observer's M1. This result is surprising in light of the mirror neuron theory, as previous research on action observation always stressed the importance of action goals for mirror motor mapping along parieto-frontal circuits to take place (Rizzolatti & Fabbri-Destro, 2008). In this view, an alternative mechanism, involving the recruitment of stored internal models may be operating here. More specifically, similar to the way that the sight of an object can recruit internal models for scaling the forces needed to handle the object (Flanagan et al., 2006) the sight of different levels of hand contraction may have induced the activation of stored internal motor representations for scaling the observed isometric forces. In this respect, the elicited M1 responses might have been driven by other pathways than those predicted by the mirror neuron theory, potentially involving the cerebellum (Bursztyn et al., 2006; Jenmalm et al., 2006).

Finally, an alternative interpretation is that the force-related motor responses, measured in the present experiments, are mainly a reflection of motor planning or action preparation which follows perceptual processes located in the visual system. More specifically, the **visual event perception theory** proposes that human observers are able to detect small variations in the form of an object's motion (namely, in terms of the shape of the motion path and the velocity profile along that path) and to use this information to visually recognize it as a specific event (Bingham, Rosenblum, & Schmidt, 1995; Bingham, 1995). According to the latter account, variations in dynamic properties of an event, like the amount of a lifted weight, can be distinguished and recognized based on a *per-*

ceptual analysis of variations in the event kinematics (McConnell, Muchisky, & Bingham, 1998; Twardy & Bingham, 2002; Wickelgren & Bingham, 2008).

Even though perceptual mechanisms might have contributed to our findings, recent evidence suggests at least some degree of motor involvement in the perception of other's actions (Pobric & Hamilton, 2006). More specifically, perturbing inferior frontal gyrus (IFG) using repetitive TMS (rTMS) impaired performance in a perceptual weight discrimination task, but not in a control task requiring the discrimination of non-biological stimuli (Pobric & Hamilton, 2006). Our findings extend these previous results, by indicating that the muscular force requirements of an observed action are reflected in the activity modulations measured in M1.

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