Springer

Dear Author,

Here are the proofs of your article.

- You can submit your corrections **online**, via **e-mail** or by **fax**.
- For **online** submission please insert your corrections in the online correction form. Always indicate the line number to which the correction refers.
- You can also insert your corrections in the proof PDF and **email** the annotated PDF.
- For fax submission, please ensure that your corrections are clearly legible. Use a fine black pen and write the correction in the margin, not too close to the edge of the page.
- Remember to note the **journal title**, **article number**, and **your name** when sending your response via e-mail or fax.
- **Check** the metadata sheet to make sure that the header information, especially author names and the corresponding affiliations are correctly shown.
- **Check** the questions that may have arisen during copy editing and insert your answers/ corrections.
- **Check** that the text is complete and that all figures, tables and their legends are included. Also check the accuracy of special characters, equations, and electronic supplementary material if applicable. If necessary refer to the *Edited manuscript*.
- The publication of inaccurate data such as dosages and units can have serious consequences. Please take particular care that all such details are correct.
- Please **do not** make changes that involve only matters of style. We have generally introduced forms that follow the journal's style.
  Substantial changes in content, e.g., new results, corrected values, title and authorship are not allowed without the approval of the responsible editor. In such a case, please contact the Editorial Office and return his/her consent together with the proof.
- If we do not receive your corrections **within 48 hours**, we will send you a reminder.
- Your article will be published **Online First** approximately one week after receipt of your corrected proofs. This is the **official first publication** citable with the DOI. **Further changes are, therefore, not possible.**
- The **printed version** will follow in a forthcoming issue.

Please note

After online publication, subscribers (personal/institutional) to this journal will have access to the complete article via the DOI using the URL: http://dx.doi.org/[DOI].
If you would like to know when your article has been published online, take advantage of our free alert service. For registration and further information go to: http://www.springerlink.com.

Due to the electronic nature of the procedure, the manuscript and the original figures will only be returned to you on special request. When you return your corrections, please inform us if you would like to have these documents returned.

Metadata of the article that will be visualized in OnlineFirst

ArticleTitle	Effect of weight-related labels on corticospinal excitability during observation of grasping: a TMS study	
Article Sub-Title		
Article CopyRight	Springer-Verlag (This will be the copyright line in the final PDF)	
Journal Name	Experimental Brain Research	
Corresponding Author	Family Name	**Fadiga**
	Particle	
	Given Name	**Luciano**
	Suffix	
	Division	D.S.B.T.A. Section of Human Physiology
	Organization	University of Ferrara
	Address	Via Fossato di Mortara 17/19, Ferrara, 44100, Italy
	Division	Department RBCS
	Organization	The Italian Institute of Technology
	Address	Via Morego 30, Genoa, Italy
	Email	fdl@unife.it
Author	Family Name	**Senot**
	Particle	
	Given Name	**Patrice**
	Suffix	
	Division	D.S.B.T.A. Section of Human Physiology
	Organization	University of Ferrara
	Address	Via Fossato di Mortara 17/19, Ferrara, 44100, Italy
	Division	Centre d'Etude de la Sensorimotricité, UMR 8194, Université Paris-Descartes/CNRS
	Organization	Institut des neurosciences et de la cognition
	Address	45 rue des Saints-Pères, Paris, 75006, France
	Email	
Author	Family Name	**D'Ausilio**
	Particle	
	Given Name	**Alessandro**
	Suffix	
	Division	Department RBCS
	Organization	The Italian Institute of Technology
	Address	Via Morego 30, Genoa, Italy
	Email	
Author	Family Name	**Franca**
	Particle	
	Given Name	**Michele**
	Suffix	
	Division	D.S.B.T.A. Section of Human Physiology
	Organization	University of Ferrara

	Address	Via Fossato di Mortara 17/19, Ferrara, 44100, Italy
	Email	
Author	Family Name	**Caselli**
	Particle	
	Given Name	**Luana**
	Suffix	
	Division	D.S.B.T.A. Section of Human Physiology
	Organization	University of Ferrara
	Address	Via Fossato di Mortara 17/19, Ferrara, 44100, Italy
	Email	
Author	Family Name	**Craighero**
	Particle	
	Given Name	**Laila**
	Suffix	
	Division	D.S.B.T.A. Section of Human Physiology
	Organization	University of Ferrara
	Address	Via Fossato di Mortara 17/19, Ferrara, 44100, Italy
	Email	

Schedule	Received	19 July 2010
	Revised	
	Accepted	9 March 2011

Abstract

Recent studies of corticospinal excitability during observation of grasping and lifting of objects of different weight have highlighted the role of agent's kinematics in modulating observer's motor excitability. Here, we investigate whether explicit weight-related information, provided by written labels on the objects, modulate the excitability of the observer's motor system and how this modulation is affected when there is a conflict between label and object's weight. We measured TMS-evoked motor potentials (MEPs) from right hand intrinsic muscles, while subjects were observing an actor lifting objects of different weights, in some trials labeled (heavy/light) in congruent or incongruent way. Results confirmed a weight-related modulation of MEPs-based kinematic cues. Interestingly, any conflict between the labels and the actual weight (i.e., explicit versus implicit information), although never consciously noticed by the observer, deeply affected the mirroring of others' actions. Our findings stress the automatic involvement of the mirror-neuron system.

Keywords (separated by '-'): Action observation - Grip force - Mirror system - Transcranial magnetic stimulation

Footnote Information

Journal: 221
Article: 2635

Author Query Form

Please ensure you fill out your response to the queries raised below and return this form along with your corrections

Dear Author

During the process of typesetting your article, the following queries have arisen. Please check your typeset proof carefully against the queries listed below and mark the necessary changes either directly on the proof/online grid or in the 'Author's response' area provided below

Query	Details required	Author's response
1.	Alaerts et al. (2010) has been changed to Alaerts et al. (2010a, 2010b) so that this citation matches the list.	
2.	van Schie et. al., 2004 has been changed to Van Schie et al. 2004 so that this citation matches the list.	
3.	Koeliwijn et al., 2008 has been changed to Koelewijn et al. 2008 so that this citation matches the list.	
4.	Knox et al. 2009 has been changed to Knox 2009 so that this citation matches the list.	
5.	References Maeda et al. (2002) are not cited in text but not provided in the reference list. Please provide references in the list or delete these citations.	
6.	pls check and confirm the Table caption and Table footer.	

Exp Brain Res
DOI 10.1007/s00221-011-2635-x

RESEARCH NOTE

Effect of weight-related labels on corticospinal excitability during observation of grasping: a TMS study

Patrice Senot · Alessandro D'Ausilio · Michele Franca · Luana Caselli · Laila Craighero · Luciano Fadiga

Received: 19 July 2010 / Accepted: 9 March 2011

Abstract Recent studies of corticospinal excitability during observation of grasping and lifting of objects of different weight have highlighted the role of agent's kinematics in modulating observer's motor excitability. Here, we investigate whether explicit weight-related information, provided by written labels on the objects, modulate the excitability of the observer's motor system and how this modulation is affected when there is a conflict between label and object's weight. We measured TMS-evoked motor potentials (MEPs) from right hand intrinsic muscles, while subjects were observing an actor lifting objects of different weights, in some trials labeled (heavy/light) in congruent or incongruent way. Results confirmed a weight-related modulation of MEPs-based kinematic cues. Interestingly, any conflict between the labels and the actual weight (i.e., explicit versus implicit information), although never consciously noticed by the observer, deeply affected the mirroring of others' actions. Our findings stress the automatic involvement of the mirror-neuron system.

P. Senot · M. Franca · L. Caselli · L. Craighero · L. Fadiga (✉)
D.S.B.T.A. Section of Human Physiology, University of Ferrara, Via Fossato di Mortara 17/19, 44100 Ferrara, Italy
e-mail: fdl@unife.it

A. D'Ausilio · L. Fadiga
Department RBCS, The Italian Institute of Technology, Via Morego 30, Genoa, Italy

Present Address:
P. Senot
Centre d'Etude de la Sensorimotricité, UMR 8194, Université Paris-Descartes/CNRS, Institut des neurosciences et de la cognition, 45 rue des Saints-Pères, 75006 Paris, France

Keywords Action observation · Grip force · Mirror system · Transcranial magnetic stimulation

Introduction

The human homolog of the monkey mirror system encodes observed movement in fine details (see Rizzolatti and Fabbri-Destro 2008). Indeed, the modulation of motor potential evoked by transcranial magnetic stimulation (TMS) during observation of transitive or intransitive action (Fadiga et al. 1995; Maeda et al. 2001; Strafella and Paus 2000) (i) is specific for the muscle involved in execution (Fadiga et al. 1995), (ii) follows a similar temporal activation pattern (Gangitano et al. 2001; Montagna et al. 2005) in an anticipatory way (Borroni et al. 2005), (iii) scales for the force needed to perform the action (Alaerts et al. 2010a), (iv) is abolished when an incongruent kinematic pattern is presented (Gangitano et al. 2004). These results have led to the conclusion that the observer's motor system does not simply "react" to the action-related visual information but rather predict the observed action (Gangitano et al. 2004).

However, a critical issue is the understanding of the peculiar contribution provided by contextual information. Recently (Alaerts et al. 2010b), showed that kinematic information alone were sufficient to evoke MEP modulation related to the force required to execute an observed grasping and lifting action. This modulation prevailed upon object-related information, such as that provided by the amount of filling of a transparent container. When kinematic and object cues provided opposite information, the encoding of force revealed by TMS in the observer's motor system depended predominantly on the observed kinematic profile. This absolute predominance of agent-dependent cues may appear somehow surprising because it has been previously shown that object-related parameters, such as orientation (Craighero et al. 1996), size (see Murray et al. 1999), material (Ellis and Lederman 1999), or even color (see Jones 1986) modulate observers' motor response.

The goal of the present experiment was twofold: first, to extend the results by (Alaerts et al. 2010b) to other types of grasping action (i.e., precision grip), to more subtle forces range and to actions performed by real agents in front of the observer. Second, to test if a more explicit, semantic, weight-related information, such as a written label, could evoke the force-related MEP modulation that object-related information was not able to evoke.

Materials and methods

Subjects

Eight healthy, right-handed (Oldfield 1971) student volunteers (7 males, 1 female, 19–34 years of age) from University of Ferrara participated to the study. Subjects gave their informed consent, and all experimental procedures were approved by the University Ethics Committee.

Stimuli

One out of six bottles at time (all sharing shape and size) was presented to the subjects during the experiment (Fig. 1a). The first two bottles were transparent and filled with a large (Visible Heavy: Vis_H) or a small amount of sand (Visible Light: Vis_L). The third and the fourth were opaque, filled with a large (Hidden Heavy: Hid_H) or a small amount of sand (Hidden Light: Hid_L). Finally, the fifth and the sixth bottles were opaque and filled with the same (large) amount of sand, but the first was labeled as "Heavy" (Labeled Heavy, Lab_H) and the second as "Light" (Labeled Light, Lab_L). Heavy bottles weighted 500 g, whereas the Light ones 100 g. In summary, during grasping/lifting observation, bottles could differ in explicit cognitive information only (Labeled), in weight-related kinematic information only (Hidden) or in both kinematic and object-related cues (Visible).

Procedure

Before the experiment, only the two transparent bottles (Vis_L and Vis_H) were presented to the subjects who were asked to experience their weight by lifting them with their right hand. Subjects were not aware of the existence of the other bottles before starting the experiment. The participant (the "observer") was seated comfortably on an armchair and faced a "scene" with black floor and background. A square metallic platform aligned with the subject's sagittal plane supported the target object.

During the experiment, the "actor" was seated fully visible on the right side in front of the subject with his right hand lying pronated on the table. At the beginning of each trial, subjects were asked to keep their eyes closed while another experimenter placed one of the six bottles on the platform, so they cannot infer the weight of the bottle from his hand kinematics during bottle placing. Subjects were then asked to open their eyes and to look at the scene. A vocal "go" signal was then provided after a delay of 3–5 s that gave time to the subject to carefully observe the scene before the movement started. The actor then reached the bottle and grasped it from the cap using the thumb and the index finger, lifted the bottle, and displaced it on the top of a platform placed a few centimeters away (Fig. 1b). The actor knew in advance the type of bottle he was going to act on, and tried to perform the action as constant and natural as possible. Caution was especially taken not to provide weight-related information to the observer with exaggerated kinematics, as can be seen, for example, when one lifts a light object while thinking it is heavy (Johansson and Westling 1988). Each bottle was presented 10 times in random order. During the whole experiment, the 3D kinematics of actor's index finger was acquired by means of an electromagnetic position-angle sensor attached to finger tip (120 Hz; Minibird 800; Ascension Technology, USA).

To keep subjects' attention focused on the lifting phase of the movement, in some trials and at random intervals after the starting of the lifting phase, a beep was generated and subjects were asked to report if the sound happened before or after the bottle was placed on the platform. Moreover, at the end of the experiment, subjects were asked to verbally answer the following two questions: "how many bottles did you see?" and "do you have any idea about their weight?".

EMG recordings and TMS

Electromyographic (EMG) activity was recorded from participants' right first dorsal interosseus muscle (FDI) using adhesive Ag–AgCl surface electrodes (Kendall GmbH, Germany) placed according to a tendon-belly bipolar disposition. Left motor cortex was stimulated using a Magstim 200 stimulator (Magstim Co., Whitland, Wales, UK). Monophasic magnetic stimuli were delivered through a figure-of-eight coil with external diameter of 7 cm. The coil was placed tangentially to the skull with the handle pointing backwards and forming a 45° angle with subjects' frontal plane. The coil was maintained in a stable position by an articulated arm (Manfrotto, Italy). Optimal scalp position and resting motor threshold (rMT) were defined

Journal : Large 221 | Dispatch : 19-3-2011 | Pages : 7
Article No. : 2635 | □ LE | □ TYPESET
MS Code : EBR-10-0438 | ✔ CP | ✔ DISK

Fig. 1 Experimental task. **a** Objects presented during the experiment. From *left to right* Visible Heavy (Vis_H), Visible Light (Vis_L), Hidden Heavy (Hid_H), Hidden Light (Hid_L), Labeled Heavy (Lab_H), Labeled Light (Lab_L). Note that the two labeled objects have the same weight (heavy) despite the different labels ("Pesante" ("Heavy"), "Leggero" ("Light"). **b** real « lift-to-displace » action as observed by the subjects. In this example, an actor reaches for a Visible Heavy bottle, grasp/lift it and place it on the *top* of a cylinder performing a natural movement

according to standard protocols (Rossini et al. 1994). Stimulation intensity was set at 120% of rMT. Inter-stimulus interval was about 30 s.

The contact between actor's fingers and the cap of the bottle was assessed through a custom-made contact sensor placed on the cap and TMS pulses was delivered at different delays (from 45 ms to 385 ms) after the touching of cap. On average, 78% of the pulses were delivered during lifting, 22% before it. Timing of touch and of TMS were recorded together with EMG (band-pass filtering, 50–1,000 Hz; sampling frequency, 2,000 Hz) and stored on a computer for off-line analysis.

Data reduction and statistics

Corticospinal (CS) excitability was calculated from MEPs area, considered as the area under the rectified EMG curve, 21–36 ms after TMS. Since EMG background activation is known to modulate MEPs amplitude (Devanne et al. 1997; Hess et al. 1987), EMG background was computed for each trial as the area under the rectified EMG signal −18 to −3 ms before TMS. Trials characterized by pre-TMS background exceeding 2.5 times the average one, as well as MEPs whose area did not exceed by 1.5 times EMG average background, were considered as bad trials and discarded from further analysis. Moreover, very huge MEPs whose area was larger than: Q3 + 1.5 * (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, Tulsa, USA), were discarded as well. Z-score of averaged MEPs areas were computed for each subject and statistics (ANOVAs and *t*-tests) were performed on these normalized data.

Results

Kinematic trajectories

Paired *t*-test analysis revealed no significant difference between conditions in loading duration, defined as the time needed for the object to be lifted by the experimenter after the fingers touched it (Mean ± Std: 198 ± 37 ms). A significant effect of weight on the velocity and acceleration peak latency (See Table 1) was instead present in the Visible ($t(7) = 6.25$; $P < 0.01$; $t(7) = 4.99$; $P < 0.01$) and Hidden ($t(7) = 4.06$; $P < 0.01$; $t(7) = 5.16$; $P < 0.01$) conditions for the two containers of the same condition. For the labeled bottles no difference was observed, being their actual weight exactly the same. From the above results, it appears that the changes in the acceleration profile occurred during the loading phase.

MEPs area

Data inspection already showed that both, individual and average MEPs, were clearly modulated by the actual weight of the lifted object (Fig. 2a).

Journal : Large 221 Dispatch : 19-3-2011 Pages : 7
Article No. : 2635 LE TYPESET
MS Code : EBR-10-0438 CP DISK

Table 1 Lift velocity and acceleration peak latencies

		Velocity (ms)	Acceleration (ms)
Light	Visible	276 ± 24	129 ± 24
	Labeled	309 ± 38	182 ± 42
	Hidden	271 ± 24	123 ± 27
Heavy	Visible	313 ± 23	172 ± 17
	Labeled	312 ± 16	171 ± 14
	Hidden	324 ± 36	184 ± 29

Latencies of actor's hand velocity and acceleration peaks during object loading and lifting for each experimental condition. Asterisks refer to statistically significant ($P < 0.05$) differences. Note, the latencies corresponding to the Heavy object for both labeled object that were actually heavy

To assess the overall effect of object-related weight cues (i.e., the degree of filling of the bottle), an ANOVA with repeated measures was conducted on MEPs areas, with factors Content Visibility (Visible vs Hidden) and Object Weight (Light vs Heavy). Results showed the effect of weight ($F(1, 7) = 14.286$, $P < 0.01$), without any significant effect of Content Visibility ($F(1,7) = 0.21$, $P = 0.7$), or significant interaction between the two factor ($F(1,7) = 0.3$, $P = 0.6$). An ANOVA was then conducted on MEPs are after removal of trials in which the TMS pulse occurred before lifting (22%). This further analysis confirmed the effect of weight ($F(1,6) = 29.5$, $P < 0.01$) without effect of Content Visibility ($F(1,6) = 0.32$, $P = 0.6$) or significant interaction ($F(1,6) = 1.29$, $P = 0.3$). These results fully agree with the results found by Alaerts et al. (2010a, b). More interestingly, we were not able to find any weight-related modulation of MEP amplitude for the Labeled condition as assessed by a *T*-test ($t(7) = 0.16$, $P > 0.05$) (Fig. 2b). It is important to stress, however, that averaged MEPs recorded during Labeled condition were significantly smaller than the averaged heavy-related MEPs recorded in Visible and Hidden conditions ($t(7) = 3.49$, $P = 0.01$, P corrected for multiple comparison with Bonferroni's corrections), despite the fact that their weight was the same (i.e., both labeled objects were heavy).

Subjective report

Subjects reported they had seen five different objects (question 1). More specifically, they all reported they had seen only one "hidden" object. When asked about the weight of the objects (question 2) they had no doubts about the two visible objects they actually experienced at the beginning of the experiment. Regarding the "only one" hidden object they remembered, they reported mixed feelings. Four subjects could not report about the weight of the "hidden" bottle. Two subjects thought it was light and one thought it was heavier than the labeled objects, and one thought it was between the visible light and the visible heavy. Regarding the labeled objects, three subjects had no idea of their weight, four reported they were both light and one thought that they had the same weight but could not say if it was heavy or light.

Discussion

The present results are two-sided. On one side, they confirm and extend the recent findings by (Alaerts et al. 2010b), by showing a significant modulation of observers' corticospinal system while they look at an actor grasping and lifting differently weighting objects (with differences in weight smaller than those reported by Alaerts et al.). On the other side, they provide relevant information about Hidden versus Labeled objects.

In the Hidden condition, the two opaque bottles could be either light or heavy. Despite the absence of object-related cues, we observed a significant modulation of MEPs

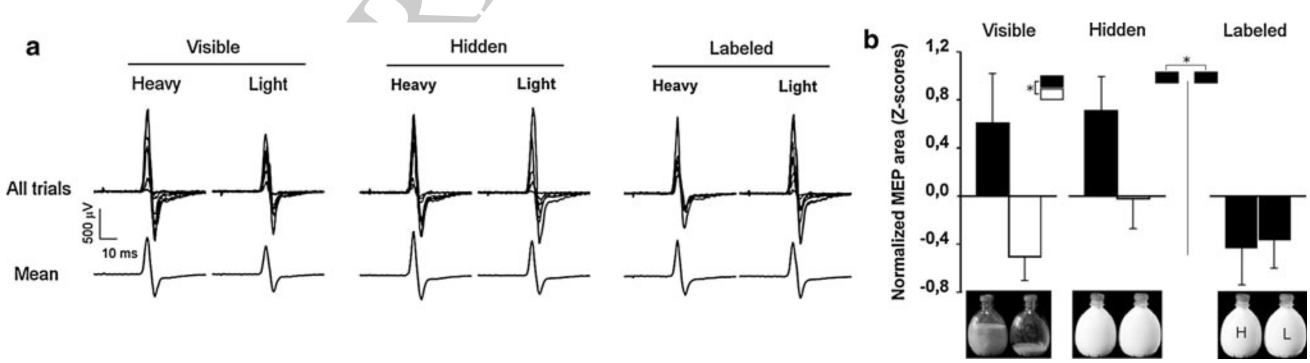

Fig. 2 Modulation of MEPs amplitude depending on the actual weight of the lifted object and on the weight-related cues. **a** Individual (*top*) and mean (*bottom*) MEPs from subject 1 for each experimental condition. **b** Grand average (mean ± standard error) of normalized MEPs area ($n = 8$) in all experimental conditions for actually heavy (*black bars*) and actually light (*white bars*) objects. *Asterisks* denote significant ($P < 0.05$) differences between conditions

Journal : Large 221 | Dispatch : 19-3-2011 | Pages : 7
Article No. : 2635 | LE | TYPESET
MS Code : EBR-10-0438 | CP | DISK

amplitude in accordance with the force required to hold the object. The relevance of kinematic information for object's weight estimation has been consistently reported (Bingham 1987; Hamilton et al. 2007; Runeson and Frykholm 1981, 1983; Shim and Carlton 1997; Shim et al. 2004). Therefore, it seems plausible that the visuo-motor system is able to automatically extract some control parameters from fine details of actor's kinematics. Interestingly, this modulation occurs even when observers are completely unaware of the presence of kinematic cues. Indeed, in the Hidden situation, subjects reported the presence of only one object, despite the fact that their corticospinal excitability was significantly scaled according to the weight of the grasped/lifted object. Moreover, the degree of this weight-dependent corticospinal modulation was not significantly different between Visible (both object-related and kinematic cues available) and Hidden conditions (only kinematic cues available), as shown by the lack of significance of the Content Visibility factor. Therefore, it seems that, at least for the case of differences in weight, motion kinematics *per se* modulates observer's corticospinal system, independently from object intrinsic properties.

Alaerts et al. (2010b) nicely showed that weight-related intrinsic object properties (e.g., degree of filling of the object) are irrelevant in coding observed force requirements. The results of our Labeled condition suggest that high-level semantic weight-related cues might be relevant in influencing the observer's motor system encoding of observed force. This influence was observed when some weight-related cues incongruence was introduced. In fact, our data show that when a mismatch existed between weight-related kinematics and explicit semantic cues (in the "Labeled" condition both bottles had the same, heavy, weight but were differently, "heavy" and "light", labeled), the motor facilitation related to heavy objects disappeared in all situations in which both cues were available. MEPs amplitude was then not significantly different from the one observed for light objects despite the kinematic cues were those related to heavy objects instead. If the labels were simply not taken into account, we would have found enhanced MEPs as for heavy objects (Hidden Heavy or Visible Heavy conditions) in both labeled conditions. On the other hand, if only labels were considered as weight-related information, we would have found a weight-related modulation similar to that of Hidden or Visible bottle pairs.

Conversely, what we found is a general inhibition of the corticospinal system, with MEPs even smaller that those recorded with light objects in the Hidden condition. Likely, the mismatch between actor kinematics and labels information might have induced an inhibition of the motor system abolishing the force encoding in all the following "labeled" trials. Once a mismatch has been detected during the experiment, both cues are considered as irrelevant. The idea that incongruent information abolishes the MEP facilitation induced by action observation is in line with previous results showing that motor resonance can vanish when a mismatch exists between the expected and the observed kinematics (Gangitano et al. 2004; Van Schie et al. 2004). On the other hand, these results contrast with previous studies in which an increase in MEP amplitude has also been reported during observation of erroneous motor actions (Aglioti et al. 2008). However, these two opposite observation can be reconciled if one consider a separate mechanisms for low-level motor resonance and high-level action understanding (Koelewijn et al. 2008). An increase in activity may reflect task failure whereas disappearance of motor resonance would rather reflect incoherence in low-level kinematic patterns, as in our experiment.

An alternative explanation derives from recent studies exploring the mapping of semantic knowledge onto the sensorimotor system. Classically, observation of real or filmed action (Fadiga et al. 1995; Maeda et al. 2002), imagination of action or observation of pictures implying motion (Urgesi et al. 2006) lead to a MEP facilitation. However, there are studies showing that listening to limb action-related verbs (Buccino et al. 2005) or looking at faces of famous athletes while categorizing them as soccer or tennis players (Candidi et al. 2010), lead to a limb-specific decrease in MEP amplitude. Candidi et al. (2010) interpret their results as a contribution toward the comprehension of the process involved in semantic derivation of categorization of others based on their motor expertise. They attribute inhibition of MEP modulation to the fact that the inferential process of categorizing stimuli semantically related to actions, such as faces or surnames of famous athletes, provide abstract information about the entire repertoire of actions within the domain of expertise of the observed athlete and not the specific motor description of a particular action. Therefore, they propose that MEP inhibition may arise from competition between these different action schemata indirectly addressed. In their study, Candidi et al. (2010) also explored whether this derivation effect was influenced by direct action observation, which typically induces corticospinal facilitation. To this aim, they asked subjects to categorize pictures of tennis and soccer athletes portrayed while performing a movement typical of their sport, a stimulus classically activating the motor system. No specific cortical facilitation was found. The authors claim that a possible explanation for this negative result is the coexistence of the categorization task, which reduced the corticospinal excitability of the same muscles and contrasted the possible facilitation contingent upon direct action observation. It is disputable if a similar mechanism determined the lack of modulation in our Labeled condition, even if it is

Journal : Large 221 | Dispatch : 19-3-2011 | Pages : 7
Article No. : 2635 | ☐ LE | ☐ TYPESET
MS Code : EBR-10-0438 | ☑ CP | ☑ DISK

improbable, since in our experimental condition the hint given by the label is not something generically addressing a pool of actions but, on the contrary, it better specifies the force necessary to execute the same action. Differentiating these two interpretations would require measuring whether the lack of modulation is already present during the first presentation of a labeled bottle or whether it vanishes after the first incoherent situation was presented. Unfortunately, no reliable information can be drawn from a single MEP.

The possibility remains that the decrease in MEPs amplitude in the Labeled condition is due to a lack of attention caused by the semantic processing of the labels. Despite this hypothesis cannot be firmly discarded here, we think that it is very unlikely for several reasons: first, as mentioned in the Material and Methods section, subjects had several seconds to read the labels on the bottle before the actor began his reaching movement toward it. The subject had then enough time to process the labels and then pay attention to the lifting phase of the action. In fact, no differences in subjects accuracy in detecting the placing of the bottle was present between labeled and other conditions. Second, if labels acted as distractors for the subject, there is some chance that the other bottle-related cues, such as the degree of filling, should have done the same. This is not the case. Finally, the secondary task in which subjects were involved (see Methods section) did not interfere with the weight-related MEP modulation and insured that subjects were focused on the action even when labels were present on the bottles.

Both interpretations proposed above point to the idea that semantic information provided by the labels is taken into account by the brain in encoding the dynamic parameters of the observed action. The fact that high-level semantic cues, such as names or labels, may influence low-level motor behavior during execution is supported by several studies showing that they could affect initiation (Króliczak et al. 2006) or performance (Gentilucci et al. 2000; Glover and Dixon 2002) of a motor response. In the Glover and Dixon experiment, "small" and "large" labels printed on objects significantly influenced fingers aperture in the early reaching phase. Jeannerod et al. (1994) also reported the case of a patient with bilateral parietal lesion that presented a deficit in hand shaping during grasping. Interestingly, the deficit disappeared during grasping of familiar objects, suggesting that semantic information were used to compensate patient's inability to transform visual object intrinsic attributes into the required motor command. What appears from our data is that, during simple action observation, the motor involvement strictly mirrors the low-level characteristics of the observed action. However, given that our subjects were likely strongly influenced, in their conscious judgement, by the wrong label, the absence of MEPs modulation in the labeled condition suggests a gating effect produced by the labels on motor mirroring. In other words, anytime a conflict is present between explicit and implicit movement-related information, the observer's motor system stops its mirroring of the observed action. If on one side this finding suggests that the mirror mechanism is not blind to semantic information (other wise, we should have found a "heavy-like" facilitation for both labeled bottles), on the other side it demonstrates that the mirror facilitation does not depend upon conscious simulation (otherwise, we should have found a label-dependent facilitation effect). This evidence strongly contradicts some interpretation of the mirror system as the neural substrate of conscious understanding (see Knox 2009) and are in agreement with some very recent neuroimaging data showing a dissociation, in terms of neural circuitry, between "mentalizing" and "mechanizing" during action observation (Spunt et al. 2011).

In summary, by this experiment, we confirm and extend previous results showing the predominance of kinematic cues over intrinsic object properties in coding force required to execute an observed lifting action. However, our data also suggest that the kinematic cues that modulate observer's motor system during observation are probably gated by high-level (via a top-down mechanism) semantic information. This information would have the power to block the mirror processing of the observed actions when incongruence exists between others' behaviors and contextual elements.

Acknowledgments Experiments were supported by Italian Ministry of Education; by the E. C. grants Contact, Robot-cub and Poeticon; by Programma di Ricerca Regione-Università and by Fondazione Cassa di Risparmio di Ferrara.

References

Aglioti SM, Cesari P, Romani M, Urgesi C (2008) Action anticipation and motor resonance in elite basketball players. Nat Neurosci 11:1109–1116

Alaerts K, Senot P, Swinnen SP, Craighero L, Wenderoth N, Fadiga L (2010a) Force requirements of observed object lifting are encoded by the observer's motor system: a tms study. Eur J Neurosci 31:1144–1153

Alaerts K, Swinnen SP, Wenderoth N (2010b) Observing how others lift light or heavy objects: which visual cues mediate the encoding of muscular force in the primary motor cortex? Neuropsychologia 48:2082–2090

Bingham GP (1987) Kinematic form and scaling: further investigations on the visual perception of lifted weight. J Exp Psychol Hum Percept Perform 13:155–177

Borroni P, Montagna M, Cerri G, Baldissera F (2005) Cyclic time course of motor excitability modulation during the observation of a cyclic hand movement. Brain Res 1065:115–124

Buccino G, Riggio L, Melli G, Binkofski F, Gallese V, Rizzolatti G (2005) Listening to action-related sentences modulates the activity of the motor system: a combined TMS and behavioral study. Cognitive Brain Res 24:355–363

Journal : Large 221 | Dispatch : 19-3-2011 | Pages : 7
Article No. : 2635 | ☐ LE | ☐ TYPESET
MS Code : EBR-10-0438 | ☑ CP | ☑ DISK

Candidi M, Vicario CM, Abreu AM, Aglioti SM (2010) Competing mechanisms for mapping action-related categorical knowledge and observed actions. Cereb Cortex 20:2832–2841

Craighero L, Fadiga L, Umiltà CA, Rizzolatti G (1996) Evidence for visuomotor priming effect. Neuroreport 8:347–349

Devanne H, Lavoie BA, Capaday C (1997) Input-output properties and gain changes in the human corticospinal pathway. Exp Brain Res 114:329–338

Ellis RR, Lederman SJ (1999) The material-weight illusion revisited. Percept Psychophys 61:1564–1576

Fadiga L, Fogassi L, Pavesi G, Rizzolatti G (1995) Motor facilitation during action observation: a magnetic stimulation study. J Neurophysiol 73:2608–2611

Gangitano M, Mottaghy FM, Pascual-Leone A (2001) Phase-specific modulation of cortical motor output during movement observation. Neuroreport 12:1489–1492

Gangitano M, Mottaghy FM, Pascual-Leone A (2004) Modulation of premotor mirror neuron activity during observation of unpredictable grasping movements. Eur J Neurosci 20:2193–2202

Gentilucci M, Benuzzi F, Bertolani L, Daprati E, Gangitano M (2000) Language and motor control. Exp Brain Res 133:468–490

Glover S, Dixon P (2002) Semantics affect the planning but not control of grasping. Exp Brain Res 146:383–387

Hamilton AFDC, Joyce D, Flanagan J, Frith C, Wolpert D (2007) Kinematic cues in perceptual weight judgement and their origins in box lifting. Psychol Res 71:13–21

Hess CW, Mills KR, Murray NM (1987) Responses in small hand muscles from magnetic stimulation of the human brain. J Physiol 388:397–419

Jeannerod M, Decety J, Michel F (1994) Impairment of grasping movements following a bilateral posterior parietal lesion. Neuropsychologia 32:369–380

Johansson R, Westling G (1988) Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. Exp Brain Res 71:59–71

Jones LA (1986) Perception of force and weight: theory and research. Psychol Bull 100:29–42

Knox J (2009) Mirror neurons and embodied simulation in the development of archetypes and self-agency. J Anal Psychol 54:307–323

Koelewijn T, van Schie HT, Bekkering H, Oostenveld R, Jensen O (2008) Motor-cortical beta oscillations are modulated by correctness of observed action. NeuroImage 40:767–775

Króliczak G, Westwood DA, Goodale MA (2006) Differential effects of advance semantic cues on grasping, naming, and manual estimation. Exp Brain Res 175:139–152

Maeda F, Chang V, Longson K, Aziz-Zadeh L, Mazziotta J, Iacoboni M (2001) Modulation of cortico-spinal excitability by goal-oriented versus non-goal-oriented hand actions. Neuroimage 13:S1223

Montagna M, Cerri G, Borroni P, Baldissera F (2005) Excitability changes in human corticospinal projections to muscles moving hand and fingers while viewing a reaching and grasping action. Eur J Neurosci 22:1513–1520

Murray DJ, Ellis RR, Bandomir CA, Ross HE (1999) Charpentier (1891) on the size-weight illusion. Percept Psychophys 61:1681–1685

Oldfield RC (1971) The assessment and analysis of handedness: the edinburgh inventory. Neuropsychologia 9:97–113

Rizzolatti G, Fabbri-Destro M (2008) The mirror system and its role in social cognition. Curr Opin Neurobiol 18:179–184

Rossini PM, Barker AT, Berardelli A, Caramia MD, Caruso G, Cracco RQ, Dimitrijevic MR, Hallett M, Katayama Y, Lucking CH (1994) Non-invasive electrical and magnetic stimulation of the brain, spinal cord and roots: basic principles and procedures for routine clinical application. report of an ifcn committee. Electroencephalogr Clin Neurophysiol 91:79–92

Runeson S, Frykholm G (1981) Visual perception of lifted weight. J Exp Psychol Hum Percept Perform 7:733–740

Runeson S, Frykholm G (1983) Kinematic specification of dynamics as an informational basis for person- and-action perception: expectation, gender recognition, and deceptive intention. J Exp Psychol 112:585–615

Shim J, Carlton L (1997) Perception of kinematic characteristics in the motion of lifted weight. J Mot Behav 29:131–146

Shim J, Carlton LG, Kim J (2004) Estimation of lifted weight and produced effort through perception of point-light display. Perception 33:277–291

Spunt RP, Satpute AB, Lieberman MD (2011) Identifying the what, why, and how of an observed action: an fMRI study of mentalizing and mechanizing during action observation. J Cogn Neurosci 23:63–74

Strafella AP, Paus T (2000) Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. Neuroreport 11:2289–2292

Urgesi C, Candidi M, Fabbro F, Romani M, Aglioti SM (2006) Motor facilitation during action observation: topographic mapping of the target muscle and influence of the onlooker's posture. Eur J Neurosci 23:2522–2530

Van Schie HT, Mars RB, Coles MGH, Bekkering H (2004) Modulation of activity in medial frontal and motor cortices during error observation. Nat Neurosci 7:549–554

Journal : Large 221 | Dispatch : 19-3-2011 | Pages : 7
Article No. : 2635 | LE | TYPESET
MS Code : EBR-10-0438 | CP | DISK