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Contextual modulation of motor resonance during the observation of everyday actions

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Neuroimaging studies on action observation suggest that context plays a key role in coding high-level components of motor behavior, including the short-term and the end-goal of an action. However, little is known about the possible role of context in shaping lower-levels of action processing such as reading action kinematics and simulating muscular activity. Here, we combined single-pulse TMS and motor-evoked potentials (MEPs) recording to explore whether top-down contextual information is capable of modulating low-level motor representations. We recorded MEPs from FDI and FCR muscles while participants watched videos about everyday actions embedded in congruent, incongruent or ambiguous contexts. Videos were interrupted before action ending, and participants were requested to predict the course of the observed action. A contextual modulation of corticospinal excitability was observed only for the FDI muscle, which is specifically involved in the execution of reaching-to-grasping movements, and whose corticospinal pathway is influenced by the observation of the very same movements. This modulation was reflected in a selective decrease of corticospinal excitability during the observation of actions embedded in incongruent as compared to congruent and ambiguous contexts. These findings indicate that motor resonance is not an entirely automatic process, but it can be modulated by high-level contextual representations.

Introduction

Comprehending other people's intentions by simply observing their actions is critical for optimally coping with them in everyday-life scenarios (Blakemore and Decety, 2001). It has been proposed (Iacoboni et al., 2005) that the ability of grasping the “why” of an action is, at least partially, made possible by the functioning of the mirror-neuron system (MNS), a fronto-parietal network that is active during both action observation and execution. On this view, the visual information from an action is mapped onto the observer's motor system, enabling the observer to immediately attribute an intentional meaning to the observed movements (Rizzolatti and Sinigaglia, 2007). However, how does the MNS transform visual information into knowledge?

From an action-oriented predictive coding approach, the role of the MNS in reading intentions from actions can be explained in terms of empirical Bayesian inference process, whereby top-down priors help to reduce uncertainty and explain away the bottom-up sensory input signal. Within this approach the most likely cause of the observed action is inferred by minimizing an error signal across different levels of a cortical hierarchy (Kilner et al., 2007). Briefly, when considering action coding, these levels are (Grafton and Hamilton, 2007; Hamilton and Grafton, 2007; Kilner et al., 2007): (i) *muscle*, which codes for the pattern of muscular activity required to execute the action; (ii) *kinematics*, which maps the movements of the effectors in space and time; (iii) *goal*, which includes the short-term transitive or intransitive aim; and (iv) *intention*, which includes the long-term purpose behind the action. For example, given a prior expectation about the goal of the actor we are observing, we can predict, on the basis of our own motor representations, the motor commands of the action and, hence, its kinematics. The comparison between the predicted and the observed kinematics generates a prediction error that is propagated across levels and serves to update information according to the actual outcome.

In keeping with this view, mirror-like activity appears to be predictive in nature, enabling people to anticipate the way an action will unfold, rather than to react to it once its long-term goal has been achieved (Abreu et al., 2012; Aglioti et al., 2008; Amoruso et al., 2014; Kilner et al., 2004, 2007; Southgate et al., 2009; Urgesi et al., 2010). Furthermore, it has been proposed that predictive processes are context-sensitive (Amoruso et al., 2014; Iacoboni et al., 2005; Kilner et al., 2007) and this is true, even in those cases where action comprehension is known to be impaired (e.g., in autistic spectrum disorders,(Boria et al., 2009; Casartelli and Molteni, 2014). In fact, actions are not perceived in isolation, but are rather context-embedded, with objects, actors, and the relationships amongst them ‘gluing together’ into a unifying scene (Amoruso et al., 2011; Ibanez and Manes, 2012).

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Evidence from functional magnetic resonance imaging (fMRI) studies suggest that context plays a key role in coding high-level components of motor behavior. For example, observing the same grasping movement embedded in two different contexts, each cueing to a different intention (grasping to drink or grasping to clean, respectively), triggered a signal increase in the inferior frontal cortex compared to observing the same movement detached from context or the context alone (Iacoboni et al., 2005). Importantly, activity within this MNS area was sensitive to the two different types of intentions. This finding was taken as evidence that the MNS actively participates in understanding the intentions underlying others' actions by coding the motor acts that are most likely to follow the observed action in a given context. But what happens when the given context instead of facilitating action recognition interferes with it?

In another fMRI study (Wurm and Schubotz, 2012), participants were required to observe everyday actions presented in neutral, compatible, or incompatible contexts (e.g., cracking an egg without context, in the kitchen or in the office, respectively). Observing actions embedded within incompatible contexts, as compared to neutral and compatible ones, increased inferior frontal cortex activity. Interestingly, when participants were asked to verbalize what action the model was performing, they did not report the actual motor act, but rather a subsequent motor act corresponding to an overarching intention (i.e., they said “making pancake” instead of “cracking an egg”), showing that contextual information modulates the concatenation of motor acts that are most likely to follow the observed action (inference of long-term goals). In this regard, incompatibility effects triggered by action-context conflict would reflect an attempt to give meaning to the observed motor act by embedding it into an overarching action which is compatible with the provided context.

Although the aforementioned studies (Iacoboni et al., 2005; Wurm and Schubotz, 2012) provide evidence about the role that contextual information plays in modulating the recognition of other's actions at a high processing level, namely, the intentional one, they do not inform about its possible role in mapping motor responses at lower levels of action processing, namely the muscle and kinematics ones. Furthermore, fMRI technique offers a unique spatial resolution for studying the neural signatures of motor resonance, however, it does not allow testing the direction of the contextual effect, in particular, whether the observed modulation of motor activation is due to excitatory or inhibitory processes.

Here, we employed single-pulse transcranial magnetic stimulation (TMS) and motor-evoked potentials (MEPs) recording during action observation to answer these questions. The basic principle of this approach is that while delivering single TMS pulses to the primary motor cortex (M1) MEPs are elicited in the contralateral target muscle. The amplitudes of these TMS-induced MEPs are modulated by action observation, replicating the muscle selectivity (Alaerts et al., 2009; Fadiga et al., 1995; Romani et al., 2005; Urgesi et al., 2006) and the temporal profile (Borroni et al., 2005; Gangitano et al., 2001; Urgesi et al., 2010) of the observed movement. This means that, while observing an action, modulations occur only in those muscles that the observer would recruit when performing the very same action, reproducing, with high temporal fidelity, the motor commands needed to execute it (for a complete review of these aspects, please refer to (Naish et al., 2014). Notably, adopting a TMS approach enables to test changes in excitatory and inhibitory corticospinal responses in a reliable fashion and, hence, determine the direction of the studied effect (Reis et al., 2008). More specifically, by measuring the amplitude of MEPs during both action observation and baseline conditions, it can be tested whether activity in a particular muscle increases or decreases from baseline during the observation of a movement involving that muscle. As MEPs represent the final output of the motor pathways, the finding of MEP amplitudes larger than baseline will reflect an excitatory process induced by action observation, while smaller ones will reflect an inhibitory process (Naish et al., 2014).

In the present study we compared the modulation of corticospinal excitability during the observation and understanding of actions embedded in congruent, incongruent and ambiguous contexts. Thus, by comparing MEPs amplitude during observation of action kinematics embedded in congruent or incongruent contexts vs. neutral, ambiguous contexts, this technique allows testing whether context enhances or reduces/suppresses motor facilitation during action observation. A temporal occlusion paradigm (Aglioti et al., 2008; Makris and Urgesi, 2014; Urgesi et al., 2012) in which action videos were stopped before the model made contact with the target object was implemented, in order to ensure that participants were only provided with the initial movement kinematics. In addition to the traditional hypothesis testing approach based on *p*-values to reject the null hypothesis of no contextual modulation of motor facilitation, we also used a Bayesian Inference approach to model the MEP data and test the strength of the contextual modulation hypothesis. Based on previous fMRI studies showing that context exerts an effect during action observation at a high processing level (i.e., the *intention* one), and in a predictive coding perspective of the MNS (Kilner et al., 2007) which suggests that top-down expectations serve to predict lower-levels of action representation, we hypothesized that context will modulate the observer's motor representation of muscle and movement kinematics. We also expected an association between the contextual modulation of motor facilitation and the individual performance during action perception, since motor coding action-context congruence should allow for a better prediction of the unfolding action.

Materials and methods

Participants

Thirteen individuals (8 women) aged 19–30 years (mean 22.69) recruited at the University of Udine took part in the experiment. The sample size required for our 2*3 (muscle*context) repeated-measures ANOVA design was determined using the G*power software (Faul et al., 2009), setting expected effects size at 0.4, alpha-level at 0.05, and desired power (1-beta) at 80%. All participants were right-handed according to a standard handedness inventory (Briggs and Nebes, 1975), had normal or corrected-to-normal visual acuity and were free from any contraindication to TMS. They gave their written informed consent prior to experimentation and received course credits for their participation in the study. The procedures were approved by the Ethics Committee of the IRCCS Eugenio Medea and were carried out in accordance with the ethical standards of the 1964 Declaration of Helsinki. None of the participants reported a history of neurological, psychiatric, or other major medical problems. No discomfort or adverse effects during TMS acquisitions were reported or noticed.

Stimuli and task

The experimental stimuli consisted of video-clips displaying the torso and hand of a woman model (aged 31 years) performing everyday-life actions. All actions were performed with the same effector (right hand) and involved the reaching-to-grasping movement of seven different objects (a bottle, a cup, a spoon, a glass, a spry cleaner, a hammer and a screw). Depending on the kinematics, considered in terms of basic reach-to-grasp movement patterns (finger prehension vs whole-hand prehension grips), each object could be grasped by the model to perform either one of two possible actions. In addition, the actions were filmed in three different contextual settings: congruent, incongruent, and ambiguous. Table 1 provides a complete list of objects, action descriptors, grip types, contexts and their possible combinations. In the congruent condition, the contextual constraints were in accordance with the observed kinematics. For example, in the case of the object “bottle”, the two possible actions were a) to pour and b) to place, each of them performed with their correspondent kinematics: