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The multiform motor cortical output: Kinematic, predictive and response coding

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ABSTRACT

Observing actions performed by others entails a subliminal activation of primary motor cortex reflecting the components encoded in the observed action. One of the most debated issues concerns the role of this output: Is it a mere replica of the incoming flow of information (kinematic coding), is it oriented to anticipate the forthcoming events (predictive coding) or is it aimed at responding in a suitable fashion to the actions of others (response coding)? The aim of the present study was to disentangle the relative contribution of these three levels and unify them into an integrated view of cortical motor coding. We combined transcranial magnetic stimulation (TMS) and electromyography recordings at different timings to probe the excitability of corticospinal projections to upper and lower limb muscles of participants observing a soccer player performing: (i) a penalty kick straight in their direction and then coming to a full stop, (ii) a penalty kick straight in their direction and then continuing to run, (iii) a penalty kick to the side and then continuing to run. The results show a modulation of the observer's corticospinal excitability in different effectors at different times reflecting a multiplicity of motor coding. The internal replica of the observed action, the predictive activation, and the adaptive integration of congruent and non-congruent responses to the actions of others can coexist in a not mutually exclusive way. Such a view offers reconciliation among different (and apparently divergent) frameworks in action observation literature, and will promote a more complete and integrated understanding of recent findings on motor simulation, motor resonance and automatic imitation.

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1. Introduction

The subliminal activation of the motor system while observing actions performed by others (i.e., motor resonance) is a widely investigated phenomenon (Grezes & Decety, 2001).

A long-term debate on the level of motor coding carried out during action observation concerns whether it reflects the observed action's kinematics or its final goal. Findings supporting the hypothesis of a direct matching between another person's body movements and our own motor representations

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have been drawn from different methodological approaches. Single cell recordings demonstrated the existence of ‘mirror neurons’ which discharged both when a monkey actually grasped 3-D objects and when it observed that action being carried out (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). In humans, single-neuron responses were likewise recorded during both action execution and observation (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010) and neuroimaging studies provided evidence that the fronto-parietal system is implicated in coupling the representations of executed and observed actions (for review see Fabbri-Destro & Rizzolatti, 2008; Giorello & Sinigaglia, 2007; Keysers, 2009; Molenberghs, Cunnington, & Mattingley, 2012; Rizzolatti & Craighero, 2004; Turella, Tubaldi, Erb, Grodd, & Castiello, 2012). A growing body of neurophysiologic studies have, moreover, demonstrated that action observation selectively activates the effector muscles involved in performing that action (for review see Fadiga, Craighero, & Olivier, 2005). The motor potentials (MEPs) evoked by transcranial magnetic stimulation (TMS) during action observation appear, in fact, to be specifically attuned to the muscles involved in the action being observed (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Sartori, Buccioni, & Castiello, 2012; Strafella & Paus, 2000; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006) and to its temporal pattern (Aglioti, Cesari, Romani, & Urgesi, 2008; Borroni & Baldissera, 2008; Borroni, Montagna, Cerri, & Baldissera, 2005; Gangitano, Mottaghy, & Pascual-Leone, 2001; Janssen, Steenbergen, & Carson, 2015; Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Montagna, Cerri, Borroni, & Baldissera, 2005; Urgesi et al., 2010). Behavioral studies have also demonstrated motor compatibility effects, showing how the observation of a finger movement that corresponds to the instructed finger movement can facilitate the response (Brass & Heyes, 2005; Liepelt, Prinz, & Brass, 2010).

On the other hand, the simulation theory specifically argues that observing another person's action is not simply a reconstruction of visual input, but an intrinsically predictive activity (Gallese & Goldman, 1998). When we observe another person's actions, we automatically anticipate their future ones. At the most basic level, humans can predict how a movement will evolve simply by watching how it was begun. For example, by observing how a person throws a dart at a dartboard, an observer can predict where the dart will land (Knoblich & Flach, 2001). An observer can likewise anticipate the type of tennis or volleyball serve that is about to be made (Abernethy, Zawi, & Jackson, 2008), predict the success of a basketball shot (Aglioti et al., 2008), foresee if a player is about to launch a real or a mimic throw (Sebanz & Shiffrar, 2009), and forecast if an action heralds a competitive or cooperative interaction (Sartori, Becchio, & Castiello, 2011). When observing action sequences, infants as well as adults show anticipatory fixations to the target areas of the displayed actions (Hunnius & Bekkering, 2010). Some studies designed to assess cortical activity of the primary motor cortex (M1) during action observation have shown that there is an anticipatory bias also in the motor response to observed actions (Candidi, Vicario, Abreu, & Aglioti, 2010; Kilner et al., 2004; Urgesi et al., 2010). For instance, motor facilitation has been found to be greater for images depicting hand actions in their

initial-middle phases than for their final stages (Gangitano et al., 2001; Urgesi et al., 2010). In this perspective, predicting another person's behavior could have immediate implications for one's own action selection system because, depending on the output of action simulation, a suitable action can be selected from a multiplicity of possible alternatives (Bekkering et al. 2009; Sartori, Xompero, Buccioni, & Castiello, 2012).

Notably, recent findings speak in favor of both the hypothesis that motor activations provide a literal copy of the observed action (Cavallo, Sartori, & Castiello, 2011; Sartori, Buccioni et al., 2012) and the hypothesis that the observer's motor system codes the distal goal of the observed acts, irrespective of the actual movements (Cattaneo, Maule, Barchiesi, & Rizzolatti, 2013). These two hypotheses are only seemingly contrasting, and can be reconciled considering that the relative influence of goal and kinematics might depend on the amount of information available to the observer (Mc Cabe, Villalta, Saunier, Grafton, & Della-Maggiore, 2014), on the time at which motor facilitation is measured (Cavallo, Buccioni, Castiello, & Becchio, 2013; Janssen et al., 2015; Lago & Fernandez-del-Olmo, 2011), and on the distinct components of the motor system which are measured (Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Barchiesi, Wache, & Cattaneo, 2012). A growing interest on dynamic human interactions has also led to the discovery of divergent forms of motor activations in effectors not primarily involved in the observed actions (Hamilton, 2013). In particular, recent evidence suggests that compatibility effects in automatic imitation can be overridden by social response preparation (Liepelt et al., 2010; Sartori, Buccioni, & Castiello, 2013).

Overall, these findings suggest that different coding levels develop during action observation. The kinematic coding, which operates at a simple motor level; the predictive coding, which anticipates the incoming actions; and the response coding, which allows an observer to prepare a response that is compatible with task demands. Crucially, an integrated view of these three levels has never been proposed, since a single effector can only be activated in one or the other modality in a given moment. The present experiment was specifically designed to disentangle the relationship between these levels and their relative contribution by measuring corticospinal excitability in multiple effectors at different timings. We adopted a paradigm involving the observation of a soccer player performing: (i) a penalty kick straight in the onlooker's direction and then coming to a full stop (Fig. 1a); (ii) a penalty kick straight in the onlooker's direction and then continuing to run (Fig. 1b); and (iii) a penalty kick to the side and then continuing to run (Fig. 1c). Single-pulse TMS was used to assess CS excitability of participants' arm and leg muscles as they watched the videos.

We hypothesized that if motor coding purely reflects what is observed, then a motor resonant activation should be found in the observers' leg muscles in all the conditions (Fig. 2a). On the other hand, if a predictive coding is performed, then leg activation should not be found when the soccer player is going to stop (Fig. 2b). Finally, if motor coding reflects the preparation of an effector-specific response, then activation should be found in the upper limb muscles, but only during the final phase of the action sequences showing the approaching ball (Fig. 2c). That is, modulations between the still and run

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