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Research report

Action observation effects reflect the modular organization of the human motor system

Pauline M. Hilt [a,*,1], *Eleonora Bartoli* [b,1], *Elisabetta Ferrari* [c], *Marco Jacono* [c], *Luciano Fadiga* [a,d] and *Alessandro D'Ausilio* [a]

[a] *IIT@UniFe Center for Translational Neurophysiology, Istituto Italiano di Tecnologia, Ferrara, Italy*
[b] *Neurosurgery Department, University of Texas Health Science Center at Houston, TX, United States*
[c] *Department of Robotics, Brain and Cognitive Science, Fondazione Istituto Italiano di Tecnologia, Genoa, Italy*
[d] *Section of Human Physiology, Università di Ferrara, Ferrara, Italy*

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ABSTRACT

Action observation, similarly to action execution, facilitates the observer's motor system and Transcranial Magnetic Stimulation (TMS) has been instrumental in exploring the nature of these motor activities. However, contradictory findings question some of the fundamental assumptions regarding the neural computations run by the Action Observation Network (AON). To better understand this issue, we delivered TMS over the observers' motor cortex at two timings of two reaching-grasping actions (precision *vs* power grip) and we recorded Motor-Evoked Potentials (4 hand/arm muscles; MEPs). At the same time, we also recorded whole-hand TMS Evoked Kinematics (8 hand elevation angles; MEKs) that capture the global functional motor output, as opposed to the limited view offered by recording few muscles. By repeating the same protocol twice, and a third time after continuous theta burst stimulation (cTBS) over the motor cortex, we observe significant time-dependent grip-specific MEPs and MEKs modulations, that disappeared after cTBS. MEKs, differently from MEPs, exhibit a consistent significant modulation across pre-cTBS sessions. Beside clear methodological implications, the multidimensionality of MEKs opens a window on muscle synergies needed to overcome system redundancy. By providing better access to the AON computations, our results strengthen the idea that action observation shares key organizational similarities with action execution.

1. Introduction

Action execution and action observation evoke similar activities in the human brain (Rizzolatti & Sinigaglia, 2016). However, there is a considerable debate around the specificity and purposes of action observation-evoked motor facilitation (D'Ausilio, Bartoli, & Maffongelli, 2015).

Dozens of studies have been published using Transcranial Magnetic Stimulation (TMS) and Motor Evoked Potentials

* *Corresponding author*. CTNSC@UniFe, Via Fossato di Mortara 17/19, Italy.
E-mail address: pauline.hilt@iit.it (P.M. Hilt).

[1] These authors contributed equally to this work.

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(MEPs) investigating how modulations of corticospinal excitability (CSE), during action observation, reflect action execution features (Fadiga, Craighero, & Olivier, 2005; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Naish, Houston-Price, Bremner, & Holmes, 2014). Some studies show that MEPs are modulated by observation of low-level motor features, such as kinematic features (e.g., fingers aperture during grasping action, Gangitano, Mottaghy, & Pascual-Leone, 2001), electromyography (EMG) temporal coupling (Borroni, Montagna, Cerri, & Baldissera, 2005; Cavallo, Becchio, Sartori, Bucchioni, & Castiello, 2012) or forces (observation of lifting of objects of different weight, Alaerts et al., 2010; Senot et al., 2011). Others works report higher level modulations, such as action goals (Cattaneo, Caruana, Jezzini, & Rizzolatti, 2009, Cattaneo, Maule, Barchiesi & Rizzolatti, 2013). For instance, MEPs modulations do not seem to map necessarily on the same effector as the one observed (Borroni & Baldissera, 2008; Finisguerra et al., 2015; Senna, Bolognini, & Maravita, 2014), suggesting their independence from low-level movement features. Lastly, studies trying to separately analyse these aspects, highlight the multi-dimensionality of Action Observation Effects (AOEs), which may depend on several details of the experimental protocol such as instructions (Mc Cabe, Villalta, Saunier, Grafton, & Della-Maggiore, 2014; Sartori, Betti, Chinellato, & Castiello, 2015), TMS trigger timing (Cavallo, Bucchioni, Castiello, & Becchio, 2013) and number of recorded muscles (Sartori et al., 2015). External influences such as learning (Catmur, Walsh, & Heyes, 2007; Catmur et al., 2008) or context (Brass, Schmitt, Spengler, & Gergely, 2007) may modulate AOEs as well.

However, apart from identifying key features of the AOEs, these studies rarely tested the reproducibility of their effects. In fact, MEPs are highly variable across time (Schmidt et al., 2009; Kiers, Cros, Chiappa & Fang, 1993) and hugely dependent on cortical states (Klein-Flügge, Nobbs, Pitcher, & Bestmann, 2013) and on spontaneous cortical oscillatory dynamics (Elswijk et al., 2010; Keil et al., 2014). More importantly, in many cases MEPs might not be the most accurate measure to explore AOEs. In fact, one basic tenet of action observation studies is that the visual appearance of actions is directly mapped onto one unique muscle activity pattern. Based on this assumption, CSE is usually recorded from few muscles at a time, during the observation of often complex kinematic configurations. CSE modulations are then used to build inferences about the functional meaning of motor activities during action observation (Naish et al., 2014). However, it is known that the same kinematic configuration can be achieved via largely different underlying muscle activation patterns (Grasso, Bianchi, & Lacquaniti, 1998; Levin, Wenderoth, Steyvers, & Swinnen, 2003).

Here we suggest that the TMS-evoked kinematic pattern (Motor Evoked Kinematics, MEK) provides a more reliable measure of motor activities induced by action observation. This assumption is based on principles of redundancy and invariance during motor execution (Flash & Hochner, 2005; Guigon, Baraduc, & Desmurget, 2007; Sporns & Edelman, 1993) and it takes into account the fact that the control of grasping actions relies upon the composition of intracortical, corticospinal, spinal and peripheral influences (Fetz, Perlmutter, Prut, Seki, & Votaw, 2002) which in turn regulate the temporal–spatial coordination of multiple agonist and antagonist muscles.

The functional output of the motor system can be extrapolated from TMS-induced MEK (Bartoli, Maffongelli, Jacono, & D'Ausilio, 2014; Finisguerra et al., 2015; Fricke et al., 2017; Gentner & Classen, 2006). Single finger MEKs are modified by physical practice (Classen, Liepert, Wise, Hallett, & Cohen, 1998) and by action observation training (Celnik et al., 2006; Stefan, Classen, Celnik, & Cohen, 2008; Stefan et al., 2005) thus reflecting short-term cortical plasticity. Whole-hand MEKs replicate the modular organization of hand functions, which are dissociable in discrete postures (Fricke et al., 2017; Gentner & Classen, 2006), requiring years of practice to be significantly changed (Gentner et al., 2010). Importantly, MEKs offer a direct measure of the functional motor output, without losing its inherent multidimensionality. This fact may have a significant impact on how we investigate the nature of AOEs (D'Ausilio et al., 2015) and could clarify to what extent action observation and action execution share similar synergistic organization principles.

To this end, we compared side-by-side MEPs and MEKs in a classical action observation protocol. Subjects observed a goal directed grasping action towards one of two simultaneously presented objects, requiring either a precision or a power grip. We recorded MEPs from 4 hand muscles as well as whole-hand MEKs at one of two possible time points during the observed reaching phase. The first time-point corresponds to maximal wrist acceleration, when limited cues are available to predict which object is going to be grasped. The second one was temporally aligned to maximal wrist velocity, occurring during the fingers opening phase, a moment at which the action goal becomes predictable (Gangitano et al., 2001). The experimental design replicates the same paradigm to evaluate the reproducibility of the AOEs. On day one, the action observation protocol was measured alone (session 1). On the second day, the action observation protocol was repeated before (session 2) and after (session 3) administering continuous Theta Burst Stimulation (cTBS) over the primary motor cortex. The action observation protocol recorded after cTBS application (session 3) was administered to evaluate a potential causal contribution of M1 excitability to both measures, MEPs and MEKs. Beside important considerations about the replicability of MEKs and MEPs, results will nourish theoretical considerations about the way by which action observation-induced motor facilitation reflects the functional, synergistic organization of the motor output.

2. Material and methods

2.1. Participants

Fifteen volunteers (5 males, 10 females, mean age and standard deviation: 25.4 ± 3.41 years) participated in the study. All participants were right handed (Edinburgh handedness inventory; Oldfield, 1971), with normal or corrected to normal vision and no contraindication to TMS according to their personal clinical history. None of them reported after-TMS undesired effects. The whole experimental procedure was approved by the local ethics committee, and was in