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Resonating with the ghost of a hand: A TMS experiment



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ABSTRACT

An impressive body of literature in the past 20 years has revealed a possible role played by cortical motor areas in action perception. One question that has been of interest is whether these areas are selectively tuned to process the actions of biological agents. However, no experiments directly testing the effects of the main characteristics identifying a biological agent (physical appearance and movement kinematics) on corticospinal excitability (CS) are present in literature. To fill this gap, we delivered single-pulse transcranial magnetic stimulation to the primary motor cortex and we recorded motor evoked potentials from contralateral hand muscles during observation of point-light-displays stimuli representing a hand having lost its physical appearance (Experiment 1) and kinematics characteristics (Experiment 2). Results showed that physical appearance, natural kinematics, and the possibility to identify the action behind the stimulus are not necessary conditions to modulate CS excitability during stimuli observation. We propose that the involvement of the motor system can be mandatory whenever the perceived movement, executed by a human, by an animal or by an object, is recognized as reproducible in its final outcome (e.g., position in space, direction of movement, posture of a body part, to-be-produced sound, specific interaction with an object, etc.), and that the peculiar relationship existing between others' actions and the actions executed by the observer could just represent the extreme in which the motor system is able to almost perfectly reproduce the observed stimulus as it unfolds and, consequently, contribute to stimulus perception in the most efficient way.

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1. Introduction

The presence of motor activity during action observation (Buccino et al., 2004; Fadiga et al., 2005) represents the clearest proof that this perceptive task automatically recruits the motor system. The privileged electrophysiological technique to study this effect is transcranial magnetic stimulation (TMS). The recording of motor evoked potentials (MEPs) from a given muscle in response to primary motor cortex (M1) stimulation is used to monitor changes in corticospinal (CS) excitability induced by the activity of various brain regions connected with M1 and involved in the concomitant task. Furthermore, the high temporal resolution of TMS is a necessary requirement to verify the dynamic (online) effects that the task has on the motor system of the participant. The fast circulation of a strong electrical current in the coil positioned on the skull induces an electric current in the brain. Consequently, when the underlying M1 cortical neurons are brought over threshold, the descending volley reaches the spinal

motoneurons, evoking a MEP detectable by standard electromyography techniques. The presence of a modulation in MEPs amplitude during the execution of perceptive or cognitive tasks indicates a variation in CS excitability induced by the task. However, given the large number of non-primary motor areas establishing excitatory connections with M1, any change in CS excitability does not tell us much about the actual brain structures underlying the facilitation. Nevertheless, a MEPs modulation that is specific to the muscles involved in the task is a clear sign of an involvement of the motor system during task execution in situations in which no overt movements are required to the participants. Many experiments have been devoted to explore the characteristics of this motor involvement, showing that perception of others' actions is constantly accompanied by motor facilitation of the observer's CS system. With the term motor resonance we specifically refer to this motor facilitation characterized by the fact that the pattern of muscle activation of the observer is very similar to the pattern of muscle contraction present during the execution of the observed action (somatotopic specificity) and that muscles activation is temporally strictly coupled with the dynamics of the observed action (high temporal fidelity). This indicates that the perceived action is subliminally reenacted (Fadiga et al., 1995; Borroni and Baldissera, 2008; Brighina et al., 2000; Clark et al.,

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2004; Gangitano et al., 2001; Montagna et al., 2005). Furthermore, studies indicated that the reenactment is automatic since somatotopic specificity is present even when the individual is not aware of the use of muscles used to perform the action (see Fadiga et al. (1995)). Moreover, in TMS experiments a necessary requirement to allow for the delivery of the pulse is the absence of any muscle preactivation which is considered an indication of a possible voluntary movement preparation. An impressive body of functional magnetic resonance imaging (for a meta-analysis see Caspers et al. (2010)), magnetoencephalography (for a review see Hari (2006)) and electroencephalography (for a review see Vanderwert et al. (2013)) studies in the past 20 years has demonstrated the presence of overlapping neural networks associated with action perception and execution. However, the presence of brain networks involved in both perception and execution does not guarantee that the perceived action is subliminally replicated with the modalities characterizing motor resonance. For this reason, we will focus the presentation of the state of the art on studies more specifically devoted to investigate, in a direct or indirect way, the effects that the perceived action has on the peripheral motor system, considering these as an index of the reenactment of that action.

Given the evidence of the exact replica of the observed action, the motor resonance effect is commonly considered the result of the encoding of action kinematic aspects (Leonetti et al., 2015). It has been proposed that this effect can be useful during imitation for motor learning (Iacoboni, 1999; Mattar and Gribble, 2005; Vogt et al., 2007) during which the acquisition of precise kinematic information about the single movements to be learned is fundamental. However, it is debated if other action features contribute to determine motor resonance.

One of the main features able to influence the observer's motor response seems to be the nature of the observed agent: the agent may be a human or an artificial device. However, agent's nature may be just inferred: it is known that motor resonance is clearly present even when the agent's hand is covered with a glove and a sleeve (Alaerts et al., 2012), or it is shown as its shadow (Alaerts et al., 2009). In these conditions, it is still recognizable as human hand. Even if no TMS experiments have directly investigated whether humanlike appearance is sufficient to evoke motor resonance, a series of behavioral experiments verified the influence that an observed action has on the execution of the same or a different action when the agent is not a human but a robot. When the agent is a human, the execution of the action is facilitated when the observed action is the same, and interfered when it is a different one (Brass et al., 2000; 2001; Craighero et al., 2002). This interference effect may be considered an indirect evidence of motor resonance: if the motor system is geared up to execute the observed movement, this should result in an interference when the observed movement is qualitatively different from the simultaneously and voluntarily executed one. When the agent is a robot, however, the interference effect is absent. This findings were firstly observed in a study in which subjects made arm movements while observing arm movements made either by another human or by a robot, which were either in the same direction (congruent) or tangential (incongruent) to the subject's own arm movements. The analysis of observers' arm movements revealed that movement variance (considered a measure of interference to the movement) differed significantly from the baseline movement condition only when subjects watched the human and not the robot making incongruent movements (Kilner et al., 2003). In an another study (Press et al., 2005) participants were required to perform a movement (e.g. opening their hand) following the presentation of a human or robotic hand in the terminal posture of a compatible movement (opened) or an incompatible movement (closed). The action was initiated faster when it was cued by the compatible movement executed by both the human and the robot, however, even when the human and robotic stimuli were of comparable size, color and brightness, the human hand had a stronger effect on performance. Other psychophysical results can be considered an indirect evidence of the influence that the observed action has on its execution, implying the presence of motor resonance only when the actor is a human, Castiello et al. (2002) found that components of manual grasping movements, such as maximum grip aperture and time to reach peak velocity, are affected by prior observation of a human model grasping an object of the same or different size and are not influenced by prior observation of a robotic hand/arm performing the same tasks. Saygin and Stadler (2012) showed participants human and robot actions. during each trial, actions were briefly occluded from view and participants were required to decide whether or not the action's timing continued naturally and coherently (i.e., in time) after occlusion. The authors suggested that to perform the task, participants were necessarily required to mentally continue the action. Results showed that the visual form of the actor affects action prediction and, possibly, the ability to reenact the observed action.

However, what differentiated humans and robots in these experiments was not only the visual form but also movement kinematics, such as the velocity profile and the trajectory of the limb. The typical velocity profile of human goal-directed hand actions is characterized by a fast-velocity initial phase and a lowvelocity final phase (Jeannerod, 1984) while, generally, robot velocity profile is characterized by constant velocity or, anyway, by a velocity profile different from the human one. Regarding the trajectory of the limb, human actions are characterized by smooth, curved shapes, while robotic motion is typically jerky and squared. Even if, as previously suggested, the motor resonance effect is commonly considered the result of the encoding of action kinematic aspects, very few studies specifically investigated the role of movement kinematics on motor resonance. In a study a paradigm similar to the one used by Saygin and Stadler (2012) was employed, people were required to infer the final position of a simple dot moving on a screen upwards or downwards. The last part of the trajectory of the dot was masked. The stimulus could either move replicating the kinematics corresponding to the upward and downward velocity profiles recorded during vertical arm pointing movements or with velocity profiles different from those recorded during a natural movement. Results showed that estimation of the final position decreased in precision and increased in variability for movements that violated the human kinematic laws (Pozzo et al., 2006). Pozzo and his colleagues (Bisio et al., 2010) have utilized the same type of stimuli to investigate the influence that natural and not natural (artificial) kinematics has on the execution of vertical arm pointing movements. Results showed that participants' movements were automatically contaminated by stimulus velocity but only when it moved according to natural kinematics (see also Bouquet et al. (2007) for a very similar experiment and analogous results). Recently, the same lab (Bisio et al., 2014) deepened the study of this problem by substituting the dot with a humanoid robot. Participants observed a humanoid robot and a human agent move their hands into a pre-specified final position or put an object into a container at various velocities. The robot could either move replicating the velocity profile of a human demonstrator previously recorded or with an artificially altered velocity profile. After action observation, participants were requested to either reach the indicated final position or to transport a similar object into another container. Results showed that participants' velocities varied consistently with stimulus velocities except when the humanoid robot violated the natural laws of motion.

Summarizing, all these data suggest that motor resonance, mainly demonstrated by interference on motor execution, seems to be independent from the physical appearance of the agent but restricted to when the agent moves with natural kinematics.

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