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Motor facilitation during observation of implied motion: Evidence for a role of the left dorsolateral prefrontal cortex

Ludovico Mineo[a], Alexander Fetterman[b], Carmen Concerto[a], Michael Warren[b], Carmenrita Infortuna[b], David Freedberg[c], Eileen Chusid[b], Eugenio Aguglia[d], Fortunato Battaglia[a,*]

[a] Department of Interprofessional Health Sciences & Health Administration, School of Health and Medical Sciences, Seton Hall University, NJ, USA
[b] Pre-clinical Sciences, New York College of Podiatric Medicine, New York, USA
[c] Department of Art History Columbia University, and Italian Academy for Advanced Studies, Columbia University, New York, USA
[d] Department of Clinical and Experimental Medicine, Psychiatry Unit, University of Catania, Italy

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ABSTRACT

The phenomenon of motor resonance (the increase in motor cortex excitability during observation of actions) has been previously described. Transcranial magnetic stimulation (TMS) studies have demonstrated a similar effect during perception of implied motion (IM). The left dorsolateral prefrontal cortex (DLPFC) seems to be activated during action observation. Furthermore, the role of this brain area in motor resonance to IM is yet to be investigated. Fourteen healthy volunteers were enrolled into the study. We used transcranial direct current stimulation (tDCS) to stimulate DLPFC aiming to investigate whether stimulation with different polarities would affect the amplitude of motor evoked potential collected during observation of images with and without IM. The results of our experiment indicated that Cathodal tDCS over the left DLPFC prevented motor resonance during observation of IM. On the contrary, anodal and sham tDCS did not significantly modulate motor resonance to IM. The current study expands the understanding of the neural circuits engaged during observation of IM. Our results are consistent with the hypothesis that action understanding requires the interaction of large networks and that the left DLPFC plays a crucial role in generating motor resonance to IM.

1. Introduction

The ability to determine the mental states of others using non-verbal cues and the capability to use this mental process to predict or explain their behavior is a crucial skill known as Theory of Mind (ToM) that enables complex social relationships. Predicting actions through the extrapolation of movement from static images, therefore, requires mental processes that enable representations of movement from actions that are only partially displayed or implied (Implied motion-IM) (Freyd, 1983; Graf et al., 2007; Parkinson et al., 2011). The illusion of motion is very well represented in works of art through the use of directional lines, gesture, position, size, contrast, and luminance. When applied to static body images these cues and characteristics are particularly effective in inducing the perception of motion (Finke et al., 1986; Freyd, 1987; Finke and Freyd, 1985; Orgs et al., 2011). Previous neuroimaging studies have suggested that the visual recognition of a movement can be obtained from the observation of a body posture with IM. These studies showed that viewing IM representations induce activation in the fusiform gyrus (Michels et al., 2005), the extrastriate body areas (Downing et al., 2001), the inferior temporal cortex (Singer and Sheinberg, 2010) and in the superior temporal sulcus (STS) (Vaina et al., 2001) indicating that observation of static images of body postures with IM activates brain areas that process perception of real movements. Furthermore, processing a static image with IM leads to the selective activation of premotor and motor cortical areas as assessed by Transcranial magnetic stimulation (TMS). TMS is a noninvasive brain stimulation technique that is used to study neural networks and to modulate brain function (Pennisi et al., 2016; Pennisi et al., 2015). Recent studies have found an increase of motor evoked potential (MEP) amplitudes in subjects receiving magnetic pulses during the observation of still images, both photographic and artistic, that incorporate the illusion of movement (Urgesi et al., 2006; Battaglia et al., 2011). This motor resonance phenomenon seems to be due to the activity of the mirror neuron systems (MNS). Mirror neurons are cortical neurons that fire during both the performance and the observation of behavior and have been considered as being crucially involved in a large array of

* Corresponding author at: Seton Hall University, 400 South Orange Avenue, South Orange, NJ 07079, USA.
E-mail address: fortunato.battaglia@shu.edu (F. Battaglia).

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highly evolved cognitive-social functions such as action understanding (Gallese et al., 1996; Rizzolatti and Craighero, 2004). The involvement of the dorsolateral prefrontal cortex (DLPFC) within the MNS and motor resonance has been marginally investigated. The DLPFC has been hypothesized as being selectively activated during action observation and imitation learning and motor preparation of actions that are not yet part of the observer's motor repertoire (Buccino et al., 2004a; Buccino et al., 2004b; Vogt et al., 2007; Vogt and Thomaschke, 2007; Higuchi et al., 2012). Furthermore, in the primate brain, DLPFC receives visual, somatosensory and visuomotor inputs (Barbas and Mesulam, 1985) and more recently, the DLPFC has also been implicated in the ToM networks (Conson et al., 2015). Still, the role of this brain area during perception of IM needs to be addressed.

In this study, we aimed to clarify whether the DLPFC plays a role in the processing of IM in a work of art. To test this hypothesis, we compared the effects of transcranial direct current stimulation (tDCS) over DLPFC on MEP size obtained during observation of static and dynamic works. tDCS is a non-invasive brain stimulation technique consisting of delivering a low, continuous electrical current to the brain area of interest by means of electrodes placed on the scalp. Typically, anodal stimulation is associated with an increase in cortical excitability, while cathodal stimulation leads to a decrease in excitability (Lefaucheur et al., 2017). Thus, we investigated the effects of different tDCS polarity applied to the left DLPFC on motor resonance hypothesizing that anodal stimulation would yield an increase in MEP amplitude during observation of IM while cathodal tDCS would result in an interference with motor resonance.

2. Materials and methods

2.1. Subjects

Fourteen healthy volunteers were enrolled into the study (mean age: 28.6 ± 5.2 years, SE, 6 Females). They were all right-handed, as assessed by a modified version of the Oldfield Handedness Questionnaire (Oldfield, 1971), and had normal or corrected to normal vision. None of the subjects had neurological or psychiatric disorders, head injuries or vision problems. None reported taking any psychoactive medications at the time of the study. None of the participants had medical implants, pregnancy or history of seizure. Written informed consent was obtained for each subject prior to the experiment. The study was conducted according to the Helsinki declaration and was approved by the local ethics committee (New York College of Podiatric Medicine). All subjects were naive to the experimental procedure and purpose of the study.

2.2. Experimental design

The subjects were seated comfortably in an armchair and were instructed to keep their eyes open in front of a computer monitor. This was a randomized sham-controlled experiment. Each participant underwent three sessions of tDCS (anodal, cathodal and sham) over left DLPFC. The order of the stimulation was counterbalanced across participants. To prevent carryover effects there was a three-day interval between the different sessions. tDCS (20 min duration, 2 mA constant current) was delivered through a saline-soaked pair of surface sponge electrodes (5 × 5 cm) using a battery-powered constant DC stimulator (Activa Tek, Inc. Salt Lake City, UT). The active electrode was placed over the left DLPFC, the F3 position according to the international 10–20 system for EEG electrode placement; the reference electrode was positioned over the contralateral supraorbital area (Fp2). For sham stimulation, the stimulator was turned off after the ramp-up phase. Before and after receiving either anodal, cathodal or sham tDCS 10 MEPs were recorded (Fig. 1, A). We then collected 10 MEPs during three experimental conditions: 1) observation of a picture of the sculpture “Abstract Figure”, 1923 by Oskar Schlemmer (no-IM); 2) observation of a picture of Umberto Boccioni, 1913 sculpture “Unique Forms of Continuity in Space” (IM); 3) observation of a plus sign (Fig. 1, B, C, D). Stimuli were presented on a computer monitor using the Presentation software (Neurobehavioral Systems, Inc.). First, the participants were instructed to focus their attention (appearance of a red triangle in the center of the monitor). After 5 s the images were presented continuously throughout the TMS paradigms. The presentation of the images was randomized.

2.3. Transcranial magnetic stimulation

TMS was delivered over the left motor cortex using a figure of 8 coil (diameter 90 mm) and a Magstim 200 magnetic stimulator (The Magstim Company, Dyfed, UK). The coil was placed flat on the skull at the optimal scalp position (hot spot) to elicit a maximal MEP in the contralateral Abductor Pollicis Brevis muscle (APB) and was held with the handle pointing backward and 45° away from the midline. The signal was amplified (Digitimer D360, Letchworth Garden, UK), filtered (band pass 20 Hz to 2.5 kHz), digitized at 5 kHz (Power Micro1401, Cambridge Electronics Design, Cambridge, UK), and stored in a laboratory computer for off-line analysis. Surface electromyography was monitored on a computer screen to ensure muscle relaxation. We tested resting motor threshold (RMT) defined as the minimum stimulation intensity necessary to evoke MEPs of 50 μV in 50% of 10 consecutive trials while the targeted hand was relaxed (Rossini et al., 2015). We then recorded 10 MEPs using a stimulation intensity of 120% RMT.

2.4. Statistical analysis

To exclude any possible effect of DLPFC tDCS stimulation on primary motor cortex excitability (MEP size) we used a two-way Repeated Measure ANOVA, main effect “stimulation” (anodal, cathodal and sham) and “time” (before and after stimulation).

The effect of tDCS on motor resonance (MEP size) during observation of IM was analyzed with a two-way ANOVA, main effect “stimulation” (anodal, cathodal and sham) and “condition” (observation ad a plus sign, statue with IM, statue without IM). Post-hoc analysis was performed with correction for multiple comparisons (Bonferroni's correction). Alpha level was set at 0.05. The statistical analysis was performed with SPSS version 22.

3. Results

All the subjects completed the study and there were no significant adverse events. tDCS did not change MEP amplitude induced by TMS. A two-way Repeated Measure ANOVA demonstrated a non-significant main effect of “stimulation”: $F_{(2,39)} = 0.6$, $p = 0.5$; “time”: $F_{(1,39)} = 0.9$, $p = 0.3$; “stimulation” × “time” interaction: $F_{(1,39)} = 0.3$, $p = 0.7$. On the contrary, DLPFC tDCS affected motor resonance during observation of implied motion in art and the effect was different across different experimental conditions (anodal, cathodal and sham stimulation). A two-way analysis of variance tested MEP size obtained during observation of a plus sign, a statue with IM and a statue with No-IM after DLPFC tDCS. The main effect of different stimulation yielded an F ratio of $F_{(2,117)} = 2.6$, $p = 0.07$ indicating a non-significant difference between anodal, cathodal and sham stimulation.

The main effect for “condition” yielded an F ratio of $F_{(2,117)} = 9.9$, $p < 0.0001$ indicating that MEP size was different across observation of images. The interaction was significant, $F_{(4,117)} = 2.6$, $p = 0.03$. A simple effects analysis for different stimulations indicated that the means for the three groups were significantly different for both anodal ($F_{(2,39)} = 8.4$, $p = 0.0009$) and sham stimulation ($F_{(2,39)} = 6$, $p = 0.005$), indicating that the observation of the IM increased the MEP size in both conditions (anodal stimulation, plus sign vs IM: $p = 0.004$, IM vs No-IM: $p = 0.005$; sham stimulation: plus sign vs IM: $p = 0.0008$, IM vs No-IM: $p = 0.001$) (Fig. 2, A and C). On the contrary, motor resonance during observation of the statue with IM was prevented by