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ORIGINAL ARTICLE

Neural circuits underlying motor facilitation during observation of implied motion

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Abstract

In the present study we used single and paired-pulse Transcranial Magnetic Stimulation (TMS) to evaluate the effect of implied motion on primary motor cortex microcircuits. We found that observation of the implied motion of a static image increases MEP amplitude and reduces short-interval intracortical inhibition (SICI), without significant modulation of intracortical facilitation and sensory-motor integration. Our results add to the existing literature on the activation of the observation-execution matching system and describe a selective modulation of GABAergic cortical microcircuits during observation of implied motion.

Keywords

Implied motion, sensorymotor integration, SICI, transcranial magnetic stimulation

History

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Introduction

Implied motion (IM) indicates the perception of movement extracted from a representation that is static in nature using cues that generate directional information (Freyd 1987). Seminal recognition memory experiments using both static objects with progressive changes in their orientation (Hubbard 1995) and pictures of irreversible movements (Freyd 1983) clearly demonstrated perception of IM. Nevertheless, little is known about the cortical networks activated during this process. Previous works demonstrated that the processing of implied dynamic information from static images induces strong activation of the prototypical visual motion areas such as the medial temporal/medial superior temporal cortex (MT/MST) (Kourtzi and Kanwisher 2000; Krekelberg et al. 2003) (Senior et al. 2000; Fawcett et al. 2007) and the dorsal stream pathway (Krekelberg et al. 2005). Furthermore, experiments using single-pulse Transcranial Magnetic Stimulation (TMS) showed that observation of a photograph picturing humans performing an action increased the amplitude of motor-evoked potentials (MEPs) (Urgesi et al. 2010; Battaglia et al. 2011), suppresses Mu rhythm and modulates event-related potentials (Sbriscia-Fioretti et al. 2013) (Umilta et al. 2013). To the best of our knowledge, the modulation of intracortical inhibitory and facilitatory circuits in sensory-motor cortex during observation of IM still needs to be investigated.

Inhibitory and excitatory intracortical circuits can be explored using paired-pulse TMS. One can test, in this way, the effect of a conditioning TMS stimulus (CS) on a test stimulus and detect both short-intracortical-inhibition (SICI) and intracortical-facilitation (ICF) (Hallett 2000). Both SICI and ICF have been largely used to investigate GABAergic and glutamatergic cortical circuits in healthy subjects and in patients with neuropsychiatric diseases (Badawy et al. 2012; Ziemann 2013; Bunse et al. 2014).

Furthermore, using short- and long-latency afferent inhibition (SAI and LAI), it is possible to explore sensorimotor integration in humans. Peripheral nerve stimulation inhibits the motor cortex at short (SAI) and long (LAI) interstimulus intervals (ISI) (Tokimura et al. 2000). SAI is modulated by cholinergic and $GABA_A$ receptor (Di Lazzaro et al. 2007) while LAI is a cortical inhibitory phenomenon that needs to be further characterized (Pirio Richardson et al. 2009). These paradigms may be used to test the functional role of sensory information in human primary motor cortex (Asanuma and Rosen 1972).

The principal objective of this study was to investigate the specific circuits underlying motor facilitation during observation of a static image that implies motion.To achieve this goal, a comprehensive neurophysiological evaluation of intracortical excitability and sensorimotor integration was performed. We hypothesized that perception of a whole body in movement in a statue (such as a running abstract figure)

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would induce an overall increase in cortical excitability even in non-observed representations.

Methods

We studied 12 healthy volunteers (six men, aged 33 ± 7.1 years; mean ± SD). All the subjects were right-handed (Oldfield 1971). The protocol was approved by the Institutional Review Board of the New York College of Podiatric Medicine.

Each participant was seated on a comfortable chair in front of a computer monitor. The experiment consisted of eliciting MEP responses during three experimental conditions: (1) observation of a plus sign; (2) observation of a picture of the sculpture ‘‘Abstract Figure’’ by Oskar Schlemmer (1923) (Sculpture no-IM: implied motion); (3) observation of a picture of Umberto Boccioni’s sculpture ‘‘Unique Forms of Continuity in Space’’ (1913) (Sculpture-IM: implied motion). We selected Boccioni’s sculpture because it so clearly sets out (as Boccioni himself and his fellow Futurists avowed) to give the impression of dynamism and speed by the forward motion on a figure in movement. On the contrary, in the case of Schlemmer’s *Abstract Figure*, we have a more ‘‘static’’ representation on an abstract figure without arms (Figure 1).

To test our research hypothesis, we selected works of art without arms and recorded MEP from a hand muscle. The presentation of the conditions (blocks) was randomized. TMS stimuli were delivered 1000 ms after images presentation.

We used a 9 cm figure-of-eight coil connected with a monophasic Magstim 200 stimulator (Magstim 200; Whitland, Dyfed, UK). The coil was placed flat on the skull with the handle pointing backwards and 45° away from the midline. It was placed at the optimal scalp position (hot spot) to elicit a maximal MEP in the contralateral Abductor Pollicis Brevis muscle (APB). Surface electromyography was monitored on a computer screen to ensure muscle relaxation. 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. Peak-to-peak amplitudes of MEPs were measured.

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. 1994). We then recorded MEP amplitude using a stimulation intensity of 110% RMT. SICI and ICF were tested by paired-TMS (Kujirai et al. 1993). SICI was induced with a CS set at 80% RMT delivered 2 ms before a test stimulus while for the induction of ICF the ISI was 10 ms. The test stimulus was adjusted to induce consistently an MEP amplitude of ~1 mV (Godfrey et al. 2013). The different ISIs were randomly selected and twenty MEPs were recorded for each condition. SICI and ICF were expressed as percentage of conditioned/unconditioned MEP. Thus, values below 100% correspond to inhibition and values above 100% correspond to facilitation. Afferent inhibition was elicited by stimulating the medial nerve at the wrist with a Digitimer D-160 stimulator (Digitimer Ltd, Welwyn Garden City, Herts, UK). Stimulus intensity was adjusted to produce a slight thumb twitch. SAI and LAI were elicited using ISIs of 25 ms and 100 ms, respectively. 20 unconditioned MEPs and 20 conditioned MEPs at each ISI were collected. The test stimulus was set to elicit ~1 mV MEP amplitude. SAI and LAI were expressed as percentage of conditioned/unconditioned MEP.

Statistical analysis

RMT and MEP amplitude were analyzed with ANOVA (main effects ‘‘Condition’’). Paired pulse experiments (SICI, ICF and SAI, LAI) were analyzed by using two-way ANOVA (main effects ‘‘Stimulation’’ and ‘‘Condition’’). *Post-hoc test* was used to test significance. All values in figures are expressed as mean ± standard error (SE). Data were analyzed

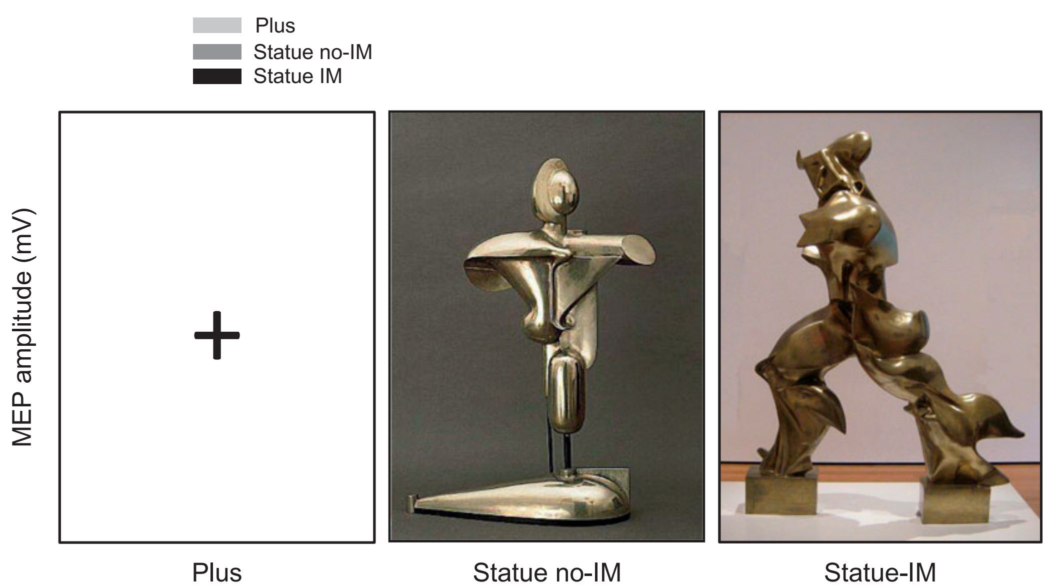

Figure 1 Experimental paradigm: TMS stimulation was performed during observation of a plus sign (plus), of a picture of the sculpture *Abstract Figure*, 1923 by Oskar Schlemmer (Sculpture no-IM: implied motion) and during observation of a picture of the sculpture *Unique Forms of Continuity in Space*, 1913 by Umberto Boccioni (Sculpture IM: implied motion).

using SPSS Version 20 (IBM Corporation, Chicago, IL, USA). Statistical significance was set at 0.05.

Results

RMT recorded in the right APB did not differ between conditions (Plus: $43 \pm 2.6\%$; Statue no-IM: $45 \pm 2.2\%$, Statue-IM: $44 \pm 2.6\%$, $F_{(2,33)} = 0.15$, $p = 0.7$) (data not showed). We next tested the effect of IM on MEP size. Observation of the picture of the Statue-IM induced an increase in MEP size (Plus: 0.43 ± 0.03 mV; Statue no-IM: 0.49 ± 0.04 mV; Statue-IM: 0.63 ± 0.04 mV, $F_{(2,33)} = 5.6$, $p = 0.008$) (Figure 2).

We then tested intracortical excitability and sensory-motor integration. In the paired-pulse paradigm TMS, the mean stimulus intensities used to obtain an MEP of $\sim$1 mV (TS) was $51 \pm 3.8\%$ for the Plus, $54 \pm 3.5\%$ for the Statue no-IM, and $52 \pm 3.6\%$, for Statue-IM. Two-way ANOVA showed a main effect for ''Stimulation'' ($F_{(1,66)} = 169.8$, $p < 0.0001$) indicating that 2 ms ISI induced inhibition while 10 ms ISI induced facilitation, and a main effect ''Condition'' ($F_{(2,66)} = 3.4$, $p = 0.03$) without a significant ''Stimulation'' X ''Condition'' interaction ($F_{(2,66)} = 0.7$, $p = 0.4$). Post-hoc analysis indicated that the amount of SICI was not different between the observation of the Plus sign and Statue no-IM ($p = 0.5$) while during observation of the Statue-IM was significantly smaller compared to the Plus sign ($p = 0.01$) and with the Statue no-IM ($p = 0.001$) (Figure 3). On the contrary, the amount of ICF was similar between the conditions (Plus: $151 \pm 7.3\%$; Statue no-IM: $145.3 \pm 8.5\%$; Statue no-IM: $159.9 \pm 11\%$; $p > 0.05$) (Figure 3). Observation of the Statue IM image did not modulate sensorimotor integration (SAI: Plus: $76.2 \pm 4.4\%$; Statue no-IM: $79.5 \pm 4.7\%$, Statue IM: $80.7 \pm 4.1\%$; LAI: Plus: $75.1 \pm 4.1\%$; Statue no-IM: $74.1 \pm 3.3\%$, Statue IM: $77.3 \pm 4.7\%$. ''Stimulation'' ($F_{(1,66)} = 0.9$, $p = 0.3$); ''Condition'' ($F_{(2,66)} = 0.3$, $p = 0.7$); Stimulation'' X ''Condition'' interaction ($F_{(2,66)} = 0.1$, $p = 0.8$) (Figure 4).

Discussion

The present study investigated whether IM information from static image of a sculpture influences intracortical excitability and sensorimotor integration. Our findings indicate that observation of an image with IM increases MEP size and reduces SICI. Furthermore, results for SAI and LAI suggest that sensorimotor integration seems not to be affected.

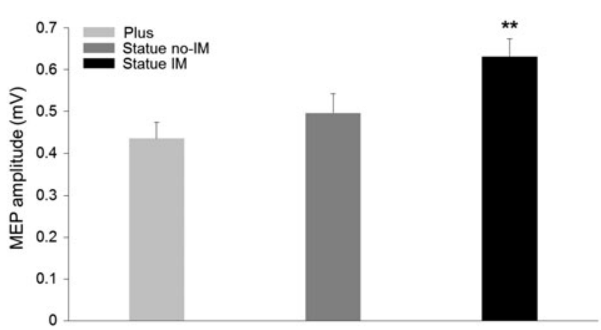

Figure 2. Observation of implied motion increased MEP size. Error bars represent standard error of the mean. **<0.01. TMS: Transcranial Magnetic Stimulation.

As previously reported (Urgesi et al. 2006), observation of IM increases MEP amplitude. We replicated these findings. Furthermore, in our study MEPs were recorded in the APB muscle even though the representation of arms in *Unique Forms of Continuity in Space* is limited at best. It is possible that observation of so humanoid and dynamic figure with wing-like forms might have conveyed an illusory perception of arm-hand movement recruiting, in this way, circuits normally activated during observation of actual hand actions (Fadiga et al. 1995; Sbriscia-Fioretti et al. 2013). We can

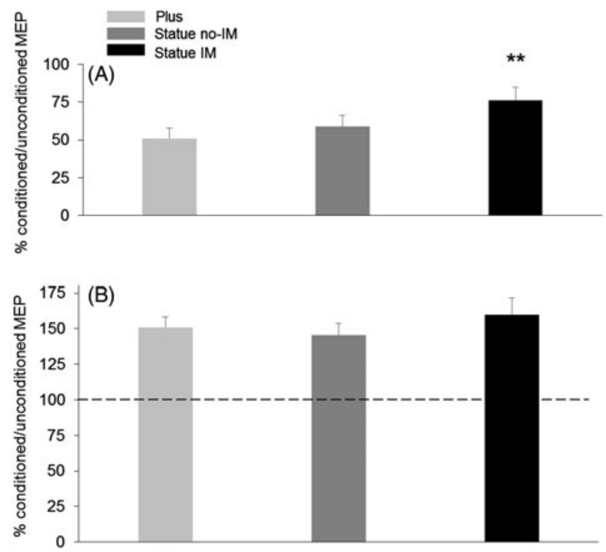

Figure 3. (A) SICI and (B) ICF. Observation of implied motion induced a decrease in the amount of SICI. There is no significant difference between conditions for ICF. Error bars represent standard error of the mean. **<0.01. SICI: short-interval intracortical inhibition; ICF: intracortical facilitation.

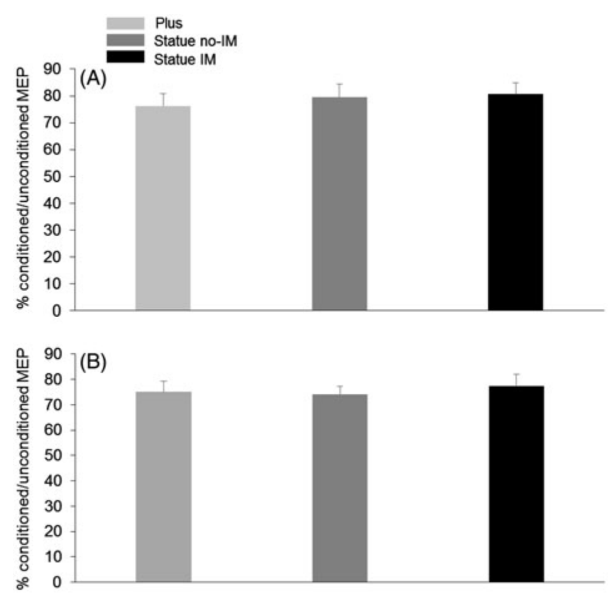

Figure 4. (A) SAI and (B) LAI. There is no significant difference between conditions. Error bars represent standard error of the mean. SAI: short-afferent inhibition; LAI: long-afferent inhibition.

speculate that observation of highly dynamic images induce overall facilitation in primary motor cortex even in representations that have no direct role in the execution of that action. General motor cortex activation may be due to the aesthetic content of the images, by enhancing the viewer's attention and therefore the tendency to grasp and manipulate (Kawabata and Zeki 2004; Urgesi et al. 2006). We showed that the observation of IM reduces SICI and induces a non-significant increase in ICF. It is likely that the activity of intracortical GABAergic microcircuits (Di Lazzaro et al. 2007) is decreased during observation of IM. This might be due either to the activation of the observation-execution matching system or to the activation of motor imagery networks that, as previously reported, have a similar modulatory effect on SICI (Patuzzo et al. 2003). SICI and SAI are TMS parameters that test two distinct inhibitory circuits in human motor cortex (Sanger et al. 2001; Di Lazzaro et al. 2007). Interestingly, IM did not affect SAI indicating a selective modulation of inhibitory circuits with specific $GABA_A$ receptor subtypes (α2- or α3-subunit) (Di Lazzaro et al. 2007).

In the present paper, we added to the knowledge of the cortical mechanisms underlying the perception of implied motion by demonstrating a selective modulation of cortical GABA-ergic microcircuits. Our results will be relevant in designing more effective, evidence-based programs involving visual art as a potential treatment for patients with both motor and cognitive deficits.

Furthermore, to generalize our findings future studies will be needed to investigate these aspects of intracortical excitability and the role of gender (Proverbio et al. 2009) in the case of observation of both moving objects and more purely abstract art forms.

Declaration of interest

The authors report no conflicts of interest.

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