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The mirror illusion induces high gamma oscillations in the absence of movement

A. Butorina [a,b], A. Prokofyev [a,c,*], M. Nazarova [d,e], V. Litvak [b], T. Stroganova [a,c]

[a] The MEG Centre, Moscow State University of Psychology and Education, Moscow, Russian Federation
[b] Wellcome Trust Centre for Neuroimaging, UCL Institute of Neurology, London WC1N 3BG, UK
[c] Psychological Institute of the Russian Academy of Education, Laboratory of Developmental Behavioural Genetics, Moscow, Russian Federation
[d] Department of Neurorehabilitation and Physical Therapy, Research Center of Neurology, Moscow, Russian Federation
[e] Centre for Cognition & Decision Making, Faculty of Psychology, Higher School of Economics, Moscow, Russian Federation

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ABSTRACT

We tested whether mirror visual feedback (MVF) from a moving hand induced high gamma oscillation (HGO) response in the hemisphere contralateral to the mirror and ipsilateral to the self-paced movement. MEG was recorded in 14 subjects under three conditions: bilateral synchronous movements of both index fingers (BILATERAL), movements of the right hand index finger while observing the immobile left index finger (NOMIRROR), and movements of the right hand index finger while observing its mirror reflection (MIRROR). The right hemispheric spatiospectral regions of interests (ROIs) in the sensor space, sensitive to bilateral movements, were found by statistical comparison of the BILATERAL spectral responses to baseline. For these ROIs, the post-movement HGO responses were compared between the MIRROR and NOMIRROR conditions. We found that MVF from the moving hand, similarly to the real movements of the opposite hand, induced HGOs (55–85 Hz) in the sensorimotor cortex. This MVF effect was frequency-specific and did not spread to oscillations in other frequency bands. This is the first study demonstrating movement-related HGO induced by MVF from the moving hand in the absence of proprioceptive feedback signaling. Our findings support the hypothesis that MVF can trigger the feedback-based control processes specifically associated with perception of one's own movements.

Introduction

Mirror hand phenomenon refers to the illusory percept of moving a hand while moving the opposite hand and viewing its reflection in a mirror. To induce the illusion the mirror is placed sagittally giving the impression that the stationary hand is performing the task. Clarifying the neurophysiological basis of the mirror hand illusion may have important clinical implications, given that mirror visual feedback (MVF) has proven to be an effective neurorehabilitation technique (Ramachandran and Altschuler, 2009).

First described by Ramachandran et al. (1992), the mirror hand phenomenon has been considered as reflecting the vital role of visual afferent feedback for hand movement control and self-awareness of one's limb movement. Indeed, the movement of one's body part is perceived not only by proprioceptive feedback from muscles and tendons but also by visual information on the body part position which is important for motor planning and on-line control of movement (Scott, 2004). In real life, somatosensory input is congruent with motor command and visual estimate of limb position. An incongruence or conflict between motor intention and afferent feedbacks about limb position produces false-perception and/or subjective feeling that the movement is not properly performed (Tsakiris et al., 2010). Regarding MVF it has been proposed that the mismatch between visual input having perfect correspondence with the motor command for self-paced movement and a lacking proprioceptive feedback from motionless hand may lead to a dominant role of visual input over proprioceptive one in subjects' awareness of their own movement (Ramachandran and Altschuler, 2009). However, the role of interaction between MVF and motor command in hand movement awareness is far from clear.

A hypothesis originating primarily from clinical studies of MVF in patients with limb paralyses implies that MVF can accelerate recovery of limb function through increasing the excitability of primary motor cortex — M1 (Ramachandran and Altschuler, 2009).

There is a large body of evidence favoring this suggestion. Physiological studies using transcranial magnetic stimulation — TMS (Garry et al., 2005) as well as EEG and MEG recordings (Praamstra et al., 2011; Tominaga et al., 2009; Touzalin-Chretien and Dufour, 2008; Touzalin-Chretien et al., 2009, 2010) investigated brain functions during motor training with MVF and showed that mirror reflection excites the motor cortex ipsilateral to the moving hand and

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[*] Corresponding author at: Sretenka 29, Moscow 107045, Russian Federation. Fax: + 74956329866.
E-mail address: vpf_child@mail.ru (A. Prokofyev).

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corresponding to its reflection. For the sake of clarity, we call this hemisphere the *mirrored* hemisphere. Similarly, the hemisphere contralateral to the movement and ipsilateral to the mirror is termed the *movement* hemisphere. Most importantly, the causal link between the MVF effect on motor potentials and increased motor cortex excitability has been proven in TMS studies demonstrating that continuous theta burst stimulation applied to the *mirrored* motor cortex disrupts the MVF effect (Nojima et al., 2012).

In addition to TMS studies lateralized readiness potentials in EEG and MEG research have been used to explore whether MVF may evoke lateralized M1 activation specifically related to the control of a moving hand (Praamstra et al., 2011; Touzalin-Chretien and Dufour, 2008; Touzalin-Chretien et al., 2009, 2010). Although the results from different research groups were contradictory, they converged on the finding of slightly increased *mirrored* motor cortical activity induced by self-produced movements observed through a mirror as compared to no-mirror condition. In line with previous findings Tominaga et al. reported that MVF from the moving hand, similarly to the real opposite hand movements, enhanced the suppression of MEG oscillations in the beta band (15–30 Hz) by median nerve stimulation. The effect was expressed in the sensors overlying *mirrored* sensorimotor cortex (Tominaga et al., 2009). Since beta band suppression was reported to indicate activation of M1 in early MEG studies (Salmelin and Hari, 1994), the authors interpreted the findings as confirming MVF effect on M1 activation. However, taking into account that the cortical source of beta suppression was recently localized to primary somatosensory (S1) cortex using more sophisticated and accurate localization technique (Gaetz and Cheyne, 2006), the results of Tominaga et al. rather indicate that MVF modulates excitatory/inhibitory balance in the *mirrored* somatosensory areas. Indeed, recently Wasaka and Kakigi (2012) reported that MVF and real hand movements induced similar changes in the amplitudes of the short- and long-latency components of somatosensory evoked magnetic fields (SEFs) in the primary and secondary somatosensory cortices of the *mirrored* hemisphere.

A question still outstanding is how MVF triggers sensorimotor circuitry in a way specifically associated with recognition of the subject's own limb movement.

There are three main lines of explanations suggested in the current literature. One possible mechanism refers to mirror neurons in inferior frontal and inferior parietal lobes. Observation of one's own movement in the mirror may activate mirror neurons sending output to the primary sensorimotor cortex in the *mirrored* hemisphere. The mirror neuron system is thought to be the basis of perception–action coupling involved in action understanding (Rizzolatti et al., 2001). The second view implies that visual feedback from the mirror goes indirectly via *mirrored* dorsal visual stream toward *mirrored* sensorimotor cortex and further engages *mirrored* corticospinal pathways (Ramachandran and Altschuler, 2009). It has been also proposed that somatosensory–visual mismatch during MVF leads to increased attentional demands for the somatosensory information from the respective hemispace, eliciting dorsolateral frontal cortex activation and secondary modulation in *mirrored* M1 and/or S1 (Wasaka and Kakigi, 2012).

The main controversy of the suggested explanations for MVF phenomenon and its effects on neuroimaging measures relates to the finding that mere observation of another person's movement can provoke changes in somatosensory and motor cortex excitability mimicking those observed for MVF. TMS and fMRI studies showed heightened sensorimotor cortex excitability while a subject inspected another person's movements (see Fadiga et al., 2005 for a review; Gazzola and Keysers, 2009), whereas exploration of neuromagnetic evoked fields to median nerve stimulation highlighted that somatosensory responses are also modulated by viewing actions made by others (Avikainen et al., 2002). In the same line of evidence, left and right hand movements performed by an actor have been shown (van Schie et al., 2008) to generate an event-related field (ERF) over the contralateral motor cortex of an observer with a similar latency to the MVF response. These studies imply that in the visual input about biological motion and/or intended action performed by another person has rather fast access to the motor cortex in line with mirror neuron hypothesis (van Schie et al., 2008). It has been suggested (Hari, 2006) that this access is mediated by the inferior or dorsolateral frontal cortex.

However, since the observer never misinterpreted another person's movements as their own, the existing neuroimaging findings on sensorimotor cortex excitation triggered by both MVF and movement observation cannot explain the illusory feeling of self-agency of mirror hand movement. Similarly, they do not clarify the specific features of M1 activation during MVF that promote limb function recovery after paralysis (see Ramachandran and Altschuler, 2009 for a review). The results rather suggest that the primary sensorimotor cortex activation on its own may not be sufficient to cause mirror hand illusion and its therapeutic effect.

From this perspective, movement-evoked high frequency gamma oscillations (HGOs) observed in intracranial EEG (ECoG), MEG and even scalp EEG studies (see Crone et al., 2011 for a review) over M1 area are of clear interest. The functional response properties of high-gamma activity are distinct from movement-related synchronization and desynchronization (ERD and ERS) of mu-rhythm in lower alpha (8–13) and beta (15–30) frequencies (Pfurtscheller et al., 2003). In EEG and MEG studies bilateral mu-rhythm suppression and subsequent rebound were considered to characterize involvement of sensorimotor cortex in movement preparation and execution. In ECoG high gamma power (60–90 Hz) responses following movements of different body parts were found to occur in a more focal topographical pattern than the alpha and beta ERD phenomena. Furthermore, somatotopically defined regions on the basis of high gamma oscillations in the sensorimotor cortex were consistent with maps generated by cortical electrical stimulation (Crone et al., 1998). The same HGOs during limb movements can be detected non-invasively by MEG (Cheyne et al., 2008; Muthukumaraswamy, 2010). In their MEG study of self-paced movements Cheyne and colleagues found that these oscillations were highly time-locked to movement onset, and observed only in the contralateral motor cortex for unilateral movements. Based on narrow somatotopic localization in M1 depending on movement of the upper and lower limbs and the lack of pre-movement gamma bursts these authors suggested that HGO could be the result of reafferent proprioceptive feedback to the primary motor cortex during movement. The lack of HGO bursts during both passive movement and movement observation however (Muthukumaraswamy, 2010) suggests that movement-related HGO may relate to active motor control processes rather than just to proprioceptive inputs. Most probably, gamma oscillations following EMG onset may reflect activation of distributed networks within primary somatosensory and motor cortices involved in the processing of afferent information requiring for ongoing feedback control of discrete self-paced movements.

Based on these observations we hypothesize that the illusory percept during MVF may relate to the presence of HGO in the *mirrored* hemisphere. In other words visual feedback from the moving mirror hand during self-initiated movement may trigger the control processes specifically associated with a person's own moving hand in the *mirrored* sensorimotor cortex.

The present study addresses this question by comparing the *mirrored* spectral responses in the illusion condition to those evoked by the same kind of movements without the mirror.

Methods

Subjects

Fourteen healthy right-handed volunteers (8 females) aged 20–33 years (mean = 25, SD = 4) took part in the study. The study was approved by the local ethics committee of the Moscow University