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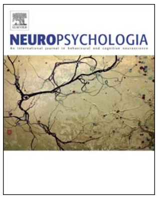

Spontaneous imitative movements induced by an illusory embodied fake hand

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ABSTRACT

In the rubber hand illusion (RHI), individuals perceive a fake hand as their own when the hidden real hand and visible fake hand are synchronously stroked. Several RHI studies have reported that visual manipulation of the embodied fake hand inversely affects the perceptual processing of the observer's own hand (e.g., thermal or pain sensitivity). In this study, we examined whether motor manipulation of the fake hand similarly affects the observer's motor system. Our study employed a novel RHI paradigm wherein stroking was interrupted by unexpected movement of the fake hand (i.e., finger spreading) while measuring electroencephalography (EEG). We found that participants often spontaneously moved their hands in accordance with the movement of the fake hand only in the RHI (synchronous) sessions. EEG analyses revealed enhanced neural activation (mu-rhythm desynchronization) of the motor system during observation of the fake hand movement. Moreover, motor activation was greater in the synchronous than in the asynchronous condition and significantly correlated with the feeling of body ownership over the fake hand. These findings provide strong behavioral and neurophysiological evidence of 'motor back projection', in which the movement of an illusory embodied body part is inversely transferred to the sensorimotor system of the observer.

1. Introduction

A striking feature of the mental world is the sensation of ownership over one's body, that is, self-perception as a coherent and unified entity separate from the external world. This feeling of body ownership is a fundamental aspect of self-consciousness (Gallagher, 2000, 2005). Although body ownership ordinarily arises from one's own body, ownership is sometimes projected onto non-corporal objects, such as in the rubber hand illusion (RHI) (Botvinick and Cohen, 1998); in the original RHI, an experimenter repeatedly strokes a participant's visually occluded hand and a visible artificial (fake) hand in synchrony, leading participants to experience touch sensations where the fake hand is stroked and consequently a sense of ownership over the fake hand (i.e., embodiment of the fake hand). Moreover, the RHI can also be induced by the visual presentation of the movement of the fake hand that matches with the active movement of the participant's hand (visuomotor synchrony) (Kalckert and Ehrsson, 2012; Longo and Haggard, 2009; Tsakiris et al., 2010; Tsakiris et al., 2006). The RHI has been intensively employed to examine the characteristics and mechanisms of body ownership (Longo and Haggard, 2012; Makin et al., 2008; Tsakiris, 2010). Recently, several studies have reported that visual manipulation of the fake hand during the RHI influences thermal or pain sensitivity of the real hand (Kanaya et al., 2012; Martini et al., 2013; Osumi et al., 2014) (see also for a critical view; Kammers et al., 2011; Mohan et al., 2012; Rohde et al., 2013). This finding suggests that perceived stimulation on the embodied fake hand is inversely influenced (back projected onto) the real hand, which we will refer to as *back projection* hereafter.

While the concept of sensory back projection has been demonstrated in previous studies, it is not known whether motor manipulation of an embodied fake limb similarly affects the observer's motor system. Clinical studies of stroke patients have reported that motor function of the affected limb is improved by mirror therapy, wherein a mirror is placed at the patient's midsagittal plane to reflect movements of the unaffected limb as if the movements are originating from the affected limb (Altschuler et al., 1999; Michielsen et al., 2011; Thieme et al., 2012). Moreover, previous studies with healthy participants have demonstrated that a mirror reflection of one hand movements affected not only somatosensory sensitivity (Bultitude et al., 2016; Romano et al., 2013) but also motor system activity of the other hand (Funase et al.,

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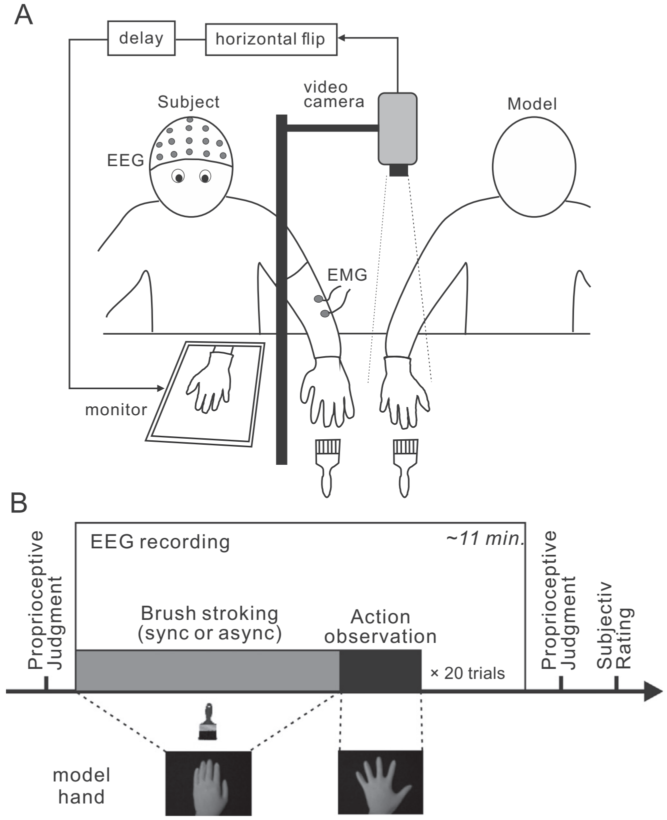

Fig. 1. Experimental setup and design. (A) To induce the rubber hand illusion, an experimenter stroked a participant's hidden left hand and a model's right hand simultaneously using two paintbrushes. Participants watched a monitor that displayed the horizontally flipped model hand. In the asynchronous condition, visuo-tactile stimuli were delivered alternately by introducing a visual feedback delay. (B) In one session (box), a stroking period (gray) followed by an action-observation period (black) were repeated. During the action-observation period, stroking was interrupted and the model hand moved suddenly and unexpectedly (simultaneous abduction and then adduction of all fingers). Before and after each session, participants made a proprioceptive judgment about their own hand to allow the assessment of proprioceptive drift. After the second proprioceptive judgment, participants rated their subjective feelings during the session using a questionnaire.

2007; Garry et al., 2005). These findings suggest the existence of back projection that the movements of the illusory embodied fake limb may enhance the motor system activity pertinent to the actual counterpart. Using electromyography (EMG), Slater et al. (2008) showed that observing the movement of an illusory embodied virtual hand could affect the muscle activity of the subject's own hand. In contrast, Schutz-Bosbach et al. (2006) reported opposite result that the observer's motor system was more enhanced in a non-illusion condition than in the RHI condition, which was measured by motor-evoked potential (MEP) with transcranial magnetic stimulation (TMS). These results are apparently contradictory and thus need further investigation. Also, these studies utilized EMG measurement (including MEP) and did not directly record the brain activity.

In the present study, we examined whether movement of a fake hand during the RHI could elicit spontaneous movement of the participant's hand and have corresponding effects on the neural motor system. Instead of a fake hand, we used the hand of an experimenter (the model hand) displayed on a monitor, which was positioned on a table facing up in front of participant to simulate the classical RHI setup (Fig. 1A). As in the conventional RHI, another experimenter repeatedly stroked both the participant's hand and the model hand in synchrony (synchronous condition) or in asynchrony (asynchronous condition) using paintbrushes. In our experiment, however, brush stroking was suddenly and unexpectedly interrupted by movement of the model hand (finger abduction and adduction) (Fig. 1B). We recorded electroencephalography (EEG) data as well as participant hand movements during the task, because EEG signals with high temporal resolution can detect brief neural response depending on bodily self-consciousness (Gonzalez-Franco et al., 2014; Padrao et al., 2016). As an objective measure of the motor system activation, we assessed the suppression of mu rhythm (8–13 Hz) power (i.e., mu-rhythm desynchronization) on EEG, which is a known phenomenon during action execution and action observation (Fox et al., 2016; Pineda, 2005; but see also Hobson and Bishop, 2016, 2017 for a critical view). Subjective questionnaire ratings and proprioceptive drift (Botvinick and Cohen, 1998) were also used as the measures for RHI. We hypothesized that (1) movement of the embodied model hand would affect motor states of the participant's hand, (2) EEG mu-rhythm desynchronization during observation of the model hand movement would be greater when participants experienced body ownership over the model hand (synchronous condition) than when they did not (asynchronous condition), and (3) the degree of mu-rhythm desynchronization would be correlated with the strength of subjective feelings of body ownership over the model hand.

2. Materials and methods

2.1. Participants

Eighteen healthy participants (6 men and 12 women; mean age ± standard deviation, 23.6 ± 5.8 years) participated in this study. Participants were blinded to the purpose of the experiment, and all but one participant were right-handed according to the Edinburgh Inventory (Oldfield, 1971). This study was approved by the institutional review board at the Kyorin University School of Medicine and conducted according to the principles and guidelines of the Declaration of Helsinki. All participants provided written informed consent prior to study participation in accordance with institutional guidelines.

2.2. Apparatus and procedures

Seated participants wore a latex glove on their left hand and placed the hand in a predetermined position on a desk (Fig. 1A). The participant's head was stabilized using a chin rest to minimize head movement. A 15-inch tablet monitor (2501A-SE, Gechic Corp., Taichung, Taiwan) was placed on the desk facing upwards in front of the participant. A wooden shelf (15 cm in depth) supported by struts was placed approximately 16 cm above participants’ forearms and the participants wore a black bib to occlude the space between the participants and shelf. This created a view for participants that the fake hand on the monitor was connected to their body (not shown in Fig. 1A). To prevent direct view of the participant's hand, a partition was placed between the participant's hand and the monitor. An experimenter's (model) right hand, also wearing a latex glove, was placed next to the participant's left hand, in order to brush the participant's and model hands as synchronously as possible by another experimenter. Top view image of the model hand was recorded by a video camera with 30 frames per second (DCR-HC62, Sony, Tokyo, Japan), flipped horizontally, delayed (only in the asynchronous condition), and displayed on the monitor. Accordingly, life-sized image of the model hand (i.e., left hand) was displayed in front of the participant. The distance between the participant's hand and the model hand image on the monitor was 25 cm. Although no artificial visual feedback delay was inserted in the synchronous condition, the inherent time delay was approximately 130 ms, which was below the reported 200-ms threshold for detecting visual feedback delay (Shimada et al., 2010). A visual feedback delay of 900 ms was added in the asynchronous condition, resulting in an actual time delay of approximately 1030 ms.

Each participant completed four experimental sessions: two synchronous and two asynchronous condition sessions. Synchronous and asynchronous sessions were administered alternately and the order was