NeuroImage 64 (2013) 216–228

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Shared electrophysiology mechanisms of body ownership and motor imagery

Nathan Evans [a,b], Olaf Blanke [a,b,c,*]

[a] Center for Neuroprosthetics, School of Life Sciences, École Polytechnique Fédérale de Lausanne, Switzerland
[b] Laboratory of Cognitive Neuroscience, Brain Mind Institute, School of Life Sciences, École Polytechnique Fédérale de Lausanne, Switzerland
[c] Department of Neurology, University Hospital Geneva, Switzerland

ARTICLE INFO

Article history:
Accepted 4 September 2012
Available online 18 September 2012

Keywords:
Body ownership
Motor imagery
Mu-band
Rubber hand illusion

ABSTRACT

Although we feel, see, and experience our hands as our own (body or hand ownership), recent research has shown that illusory hand ownership can be induced for fake or virtual hands and may be useful for neuroprosthetics and brain–computer interfaces. Despite the vast amount of behavioral data on illusory hand ownership, neuroimaging studies are rare, in particular electrophysiological studies. Thus, while the neural systems underlying hand ownership are relatively well described, the spectral signatures of body ownership as measured by electroencephalography (EEG) remain elusive. Here we induced illusory hand ownership in an automated, computer-controlled manner using virtual reality while recording 64-channel EEG and found that illusory hand ownership is reflected by a body-specific modulation in the mu-band over fronto-parietal cortex. In a second experiment in the same subjects, we then show that mu as well as beta-band activity in highly similar fronto-parietal regions was also modulated during a motor imagery task often used in paradigms employing non-invasive brain–computer interface technology. These data provide insights into the electrophysiological brain mechanisms of illusory hand ownership and their strongly overlapping mechanisms with motor imagery in fronto-parietal cortex. They also highlight the potential of combining high-resolution EEG with virtual reality setups and automatized stimulation protocols for systematic, reproducible stimulus presentation in cognitive neuroscience, and may inform the design of non-invasive brain–computer interfaces.

Introduction

Human self-consciousness has become an increasingly prominent issue in the cognitive neurosciences in recent years (Blanke and Metzinger, 2008; Christoff et al., 2011; Gallagher, 2000). Whereas earlier research focused mainly on higher-level aspects such as memory, personality, or language and how these functions relate to the self and self-consciousness (Gillihan and Farah, 2005; Legrand and Ruby, 2009; Northoff et al., 2006), recent studies have started to investigate more basic aspects of self-consciousness, especially how we experience and perceive our body. Such mechanisms of bodily self-consciousness consist of brain mechanisms encoding the different multisensory and sensorimotor states of the body (Berlucchi and Aglioti, 1997, 2009; Botvinick, 2004; Damasio, 2000; Jeannerod, 2006, 2007; Vogeley and Fink, 2003).

One aspect that has been investigated intensively over the last decade is the experience that our body and its parts belong to us and are not those of other people, so-called body ownership. Ownership for one's hand has been proposed to constitute a crucial aspect of bodily self-consciousness (De Vignemont, 2011; Gallagher, 2000; Makin et al., 2008; Tsakiris, 2010) and an increasing number of empirical data on the neural underpinnings of body ownership have pointed to the importance of multisensory integration of visual, tactile and proprioceptive signals (Botvinick, 2004; Botvinick and Cohen, 1998; Ehrsson et al., 2005; Tsakiris and Haggard, 2005). A widely used paradigm to study the multisensory perception of upper limbs is the rubber hand illusion (RHI; Botvinick and Cohen, 1998) where participants watch an artificial hand (visual cue) being stroked by a paintbrush in synchrony with stroking on their own corresponding and occluded hand (tactile cue). This visuo-tactile manipulation alters bodily experience, inducing the illusion that the artificial hand being touched is one's own hand (measured by questionnaire ratings) and is generally associated with a measurable mislocalization of the participant's hand towards the fake hand. The illusion does not occur when the stroking provided to the real hand and the artificial hand is not synchronous, when the fake hand does not match the posture of the real hand, or when control objects are stroked (Botvinick and Cohen, 1998; Ehrsson et al., 2004; Tsakiris and Haggard, 2005).

To investigate the brain mechanisms of illusory hand ownership, most neuroimaging studies have manipulated the synchrony of experimenter-applied visuo-tactile stroking and the congruence of posture or handedness of the fake and real hands. Using fMRI, illusory ownership as induced by synchronous visuo-tactile stroking on congruent fake hand postures was found to be reflected by BOLD activity in bilateral premotor cortices (Ehrsson et al., 2004), cerebellum (Ehrsson et al., 2005), and intraparietal cortices (Ehrsson et al.,

* Corresponding author at: Faculty of Life Sciences, École Polytechnique Fédérale de Lausanne, Station 19, CH-1015 Lausanne, Switzerland.
E-mail address: olaf.blanke@epfl.ch (O. Blanke).

1053-8119/$ – see front matter © 2012 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.neuroimage.2012.09.027

2004, 2005). If the fake hand is threatened by bringing a needle near to it, other studies found that activity in the supplementary motor area (Ehrsson et al., 2007) and posterior parietal regions (Lloyd et al., 2006) reflects illusory ownership. In addition, activity in bilateral anterior insular and anterior cingulate cortices (Ehrsson et al., 2007) or activity in premotor cortex and cerebellum (Ehrsson et al., 2004) was found to correlate with the strength of ownership illusion (as measured by questionnaire ratings). In a PET study, Tsakiris et al. (2007) reported that activity in the right posterior insula, sensorimotor cortices (precentral and postcentral gyri), as well as primary somatosensory cortex was associated with illusory hand ownership. Moreover, activity in the right insula and left somatosensory cortex correlated with the magnitude of proprioceptive drift (Tsakiris et al., 2007), a phenomenon classically associated with illusory hand ownership (Botvinick and Cohen, 1998; but see also Rohde et al., 2011). Finally, clinical studies in stroke patients showed a relationship between lesion location and damaged connections between premotor, frontal operculum, basal ganglia, parietal, and prefrontal cortices with the inability to experience illusory ownership for a fake hand (Zeller et al., 2011). To summarize, neuroimaging studies across a variety of RHI setups and imaging techniques (e.g. fMRI, PET, lesion mapping) have revealed a wide network of brain regions associated with illusory body ownership during the RHI. These regions include the intraparietal cortex, primary somatosensory cortex (precentral and postcentral gyri), the ventral premotor cortex, the right insular lobe, the anterior cingulate cortex, and the cerebellum (Ehrsson et al., 2004, 2005, 2007; Lloyd et al., 2006; Tsakiris et al., 2007; Zeller et al., 2011).

Concerning electrophysiological correlates of illusory hand ownership, several EEG studies using somatosensory evoked potentials (SEPs) or frequency analysis have also been carried out. For example, Kanayama et al. (2007, 2009) reported that gamma-band oscillations over parietal scalp regions varied according to the strength of illusory hand ownership in a RHI-like paradigm. These authors observed an increase in inter-electrode synchrony in the lower gamma-band (30–50 Hz) over parietal scalp regions during the integration of tactile and visual cues in peripersonal space. In an ERP study, Press et al. (2008) showed enhancement of the N140 and late somatosensory SEP components (evoked by hand tapping) after a period of synchronous stroking of a rubber hand, likely reflecting activation in somatosensory regions of the parietal cortex and/or premotor cortex. Related work using a different illusory hand ownership paradigm (numbness illusion) measured SEPs and implicated primary somatosensory cortex (Dieguez et al., 2009) based on the observation that the earliest cortical SEP component after median nerve stimulation (N20 component) was enhanced and correlated in strength with illusory ownership. Across these electrophysiological studies employing diverse experimental procedures, these data reveal that premotor and parietal cortex activity as well as gamma-band oscillations have most consistently been linked to illusory hand ownership.

Yet, in a number of related sensorimotor tasks, neural oscillations over central areas including premotor, motor, and somatosensory cortices have been linked rather to the mu rhythm (8–13 Hz oscillations). Sensorimotor tasks (Pineda, 2005), motor action execution, inhibition, and observation (Gastaut, 1952; Howe and Sterman, 1972; Niedermeyer and Lopes da Silva, 1993) are reflected in such mu oscillations. Additionally, both intracranial electrophysiology (Gastaut and Bert, 1954; Mukamel et al., 2010; Tremblay et al., 2004) and surface EEG (Cochin et al., 1999, 1998) consistently show comparable mu rhythm suppression during both the execution and the observation of different movements. Mu oscillations have also been investigated with respect to motor imagery (review in Neuper et al., 2006) and have been linked to mu suppression in parietal cortex, premotor, and primary sensorimotor areas (Pfurtscheller and Neuper, 1997; Pfurtscheller et al., 1997a). These oscillations during hand motor imagery have also been decoded online in non-invasive brain–computer interfaces (Pfurtscheller et al., 1997b). The mu rhythm is also modulated by touch (Pfurtscheller, 1981), the observation of touch of another person (Cheyne et al., 2003), and covaries with the BOLD signal in dorsal premotor, inferior parietal, and primary somatosensory cortices during both action execution and observation (Arnstein et al., 2011). More recently, it has also been shown that changes in body ownership for a full body as seen in a virtual reality environment are reflected in mu-activity in premotor, sensorimotor, and medial prefrontal cortices (Lenggenhager et al., 2011).

To summarize, despite this frequential and anatomical convergence of illusory hand ownership and hand motor imagery, the spatial and spectral relationship between motor imagery and illusory hand ownership has not been studied directly in the same individuals. Moreover, hand motor imagery is often used in non-invasive brain–computer interfaces (e.g. Pfurtscheller and Neuper, 2001) and it has recently been speculated that illusory ownership over virtual and prosthetic limbs may benefit neuroprosthetics and neuro-rehabilitation (Ehrsson et al., 2008; Marasco et al., 2011). Here, we designed a virtual reality environment with automatized, machine-controlled visuo-tactile stimulation to induce changes in illusory hand ownership while recording 64-channel EEG. Using this setup, we first analyzed cortical oscillations and their neural generators reflecting changes in illusory body ownership. Next, we investigated – in the same subjects – brain oscillations and their neural generators during a hand motor imagery paradigm (e.g. Pfurtscheller et al., 1997b) and directly compared ownership-related brain activations with oscillations present during motor imagery.

Materials and methods

Participants

12 healthy, right-handed participants were recruited (ages 22.7 ± 4.1 *mean* ± *SD*; 3 females). All participants had normal or corrected-to-normal vision and gave informed consent prior to participation. The study was undertaken in accordance with the ethical standards as defined in the Declaration of Helsinki and was approved by the local ethics research committee at the University of Lausanne.

Tactile stimulation

Tactile stimulation was provided with a total of eight button-style vibration motors (Precision Microdrives, London, UK) affixed in a line to the palms of the participants' hands (Fig. 1A). On each hand, a custom-made set of four vibration motors (12 mm diameter; 1.7 g; maximum rotation frequency 150 Hz) was placed with an inter-vibrator distance of 2 cm. The motors were programmed to vibrate in sequence to simulate a continuous, stroke-like movement lasting 450 ms (75 ms per motor; 50 ms inter-motor vibration pause). This type of sequence was chosen to automatize the stroking patterns that are generally used to manually stroke participants' hands to induce the RHI (i.e. Botvinick and Cohen, 1998; Ehrsson et al., 2004). The direction of the stroking sequence was either inward, toward a central fixation cross (6 subjects), or outward, away from the fixation cross (6 subjects). An inter-stroke interval of 400 ms was inserted between strokes to aid in perceiving the sequence of vibrations as a single motion.

Stimuli and virtual reality

Visual stimuli were rendered in stereo (XVR; VRMedia, Pisa, Italy) on a Fakespace Wide5 head-mounted display (HMD; Fakespace Labs, Mountain View, CA, USA). The HMD displayed a virtual scene with either two virtual arms or two virtual non-body control objects visually projected as extending from the body and resting on a tabletop (Figs. 1B, C). Four virtual spheres on each palm of the two virtual arms (or two virtual control objects) visually represented the four vibration motors on the real hands. Visual "vibrations" were represented by changing the virtual motor's color from white to red and animating it to visually jitter between