Neuroscience 216 (2012) 110–122

EARLY AND LATE ACTIVITY IN SOMATOSENSORY CORTEX REFLECTS CHANGES IN BODILY SELF-CONSCIOUSNESS: AN EVOKED POTENTIAL STUDY

J. E. ASPELL,[a]* E. PALLUEL[a] AND O. BLANKE[a,b]

[a] Laboratory of Cognitive Neuroscience, Ecole Polytechnique Fédérale de Lausanne (EPFL), Lausanne, Switzerland

[b] Department of Neurology, University Hospital, Geneva, Switzerland

Abstract—How can we investigate the brain mechanisms underlying self-consciousness? Recent behavioural studies on multisensory bodily perception have shown that multisensory conflicts can alter bodily self-consciousness such as in the ''full body illusion'' (FBI) in which changes in self-identification with a virtual body and tactile perception are induced. Here we investigated whether experimental changes in self-identification during the FBI are accompanied by activity changes in somatosensory cortex by recording somatosensory-evoked potentials (SEPs). To modulate self-identification, participants were filmed by a video camera from behind while their backs were stroked, either synchronously (illusion condition) or asynchronously (control condition) with respect to the stroking seen on their virtual body. Tibial nerve SEPs were recorded during the FBI and analysed using evoked potential (EP) mapping. Tactile mislocalisation was measured using the crossmodal congruency task. SEP mapping revealed five sequential periods of brain activation during the FBI, of which two differed between the illusion condition and the control condition. Activation at 30–50 ms (corresponding to the P40 component) in primary somatosensory cortex was stronger in the illusion condition. A later activation at ~110–200 ms, likely originating in higher-tier somatosensory regions in parietal cortex, was stronger and lasted longer in the control condition. These data show that changes in bodily self-consciousness modulate activity in primary and higher-tier somatosensory cortex at two distinct processing steps. We argue that early modulations of primary somatosensory cortex may be a consequence of (1) multisensory integration of synchronous vs. asynchronous visuo-tactile stimuli and/or (2) differences in spatial attention (to near or far space) between the conditions. The later activation in higher-tier parietal cortex (and potentially other regions in temporo-parietal and frontal cortex) likely reflects the detection of visuo-tactile conflicts in the asynchronous condition.

Key words: body perception, self-consciousness, somatosensory, electroencephalography, multisensory integration.

INTRODUCTION

Body ownership (the sense that my body belongs to me) is a crucial feature of bodily self-consciousness, the nonconceptual and pre-reflective representation of body-related information (Gallagher, 2005; Jeannerod, 2007; Blanke and Metzinger, 2009). Recent work shows that this apparently deeply rooted aspect of human experience is, to some degree, modifiable. Thus, visuo-tactile conflicts can induce measurable changes in self-attribution of a fake hand in the rubber hand illusion (Botvinick and Cohen, 1998), and in self-identification with a whole virtual body in the full body illusion (FBI) (Lenggenhager et al., 2007, 2009); see also (Ehrsson, 2007). Changes in tactile perception have also been found to accompany changes in bodily self-consciousness: a recent study demonstrated the modulation of touch by measuring crossmodal congruency effects (CCEs) – derived from repeated reaction time (RT) and accuracy measurements – during the FBI (Aspell et al., 2009). This study demonstrated that the modulation of self-identification was also reflected in differences in CCE magnitude, providing strong evidence for the mislocalisation of touch towards a virtual body during the illusion. A similar CCE demonstration of tactile mislocalisation was found when participants viewed a rubber hand (Pavani et al., 2000; Heed et al., 2010). In the present study we investigated whether these changes in self-identification and tactile perception during the FBI are accompanied by changes in somatosensory cortex.

Not much is known about which brain mechanisms underlie the induced changes in self-identification with a virtual body or avatar, but three recent FBI studies have begun to answer this question. The first, using frequency analysis and high resolution electroencephalography (EEG), showed that primary somatosensory cortex and medial prefrontal cortex reflect changes in self-identification and self-location during the FBI (Lenggenhager et al., 2011) and the second, an functional magnetic resonance imaging (fMRI) study, revealed that activation of the right temporo-parietal junction is modulated by

*Corresponding author. Address: Department of Psychology, Faculty of Science and Technology, Anglia Ruskin University, Cambridge, CB1 1PT, United Kingdom. Tel: +44-1223-363271x2258.
E-mail addresses: jane.aspell@anglia.ac.uk, jane.aspell@epfl.ch (J.E. Aspell).

Abbreviations: ANOVA, analyses of variance; CCE, crossmodal congruency effects; EEG, electroencephalography; EP, evoked potential; FBI, full body illusion; GFP, global field power; HMD, head mounted display; LED, light emitting diode; RHI, rubber hand illusion; RT, reaction time; SEP, somatosensory-evoked potential; TPJ, temporo-parietal junction.

0306-4522/12 $36.00 © 2012 IBRO. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.neuroscience.2012.04.039

changes in self-location (Ionta et al., 2011). Another fMRI study of a similar FBI, the ''body swap'' illusion found that activation in the left intraparietal and bilateral ventral premotor cortices (and left putamen) was greater in the illusion condition than in the asynchronous control condition (Petkova Valeria et al., 2011). Differences between the findings of these FBI studies are likely due to variations in the experimental setup (viewing a mannequin vs. an animated avatar; first person vs. third person perspective, etc.) and in the methods used to measure brain activity. Related neuroimaging studies of self-attribution of a fake hand during the rubber hand illusion (RHI) implicated a wide network of similar brain regions including the intraparietal cortex, primary somatosensory cortex, the right temporo-parietal junction, the ventral premotor cortex and the right insular lobe (Ehrsson et al., 2004, 2005, 2007; Tsakiris et al., 2007, 2008).

Parietal cortex has also been implicated in self-attribution by studies employing somatosensory-evoked potentials (SEPs) and frequency analysis. For example, (Kanayama et al., 2007, 2009) reported that gamma band oscillations (40–50 Hz) over parietal scalp regions varied according to RHI strength. One SEP study (Press et al., 2008) showed enhancement of a late somatosensory SEP component (evoked by hand tapping) after a period of synchronous stroking of a rubber hand, likely reflecting activation of higher-tier somatosensory regions in parietal cortex (and/or premotor cortex), whereas a different illusion paradigm using SEPs 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. In summary, these data, using a variety of tasks and neuroimaging methods support an implication of parietal cortex in self-identification, but do not enable us to distinguish between activity changes in primary somatosensory cortex vs. higher-tier regions in parietal cortex.

Here, to specifically investigate the role of somatosensory cortex, we investigated the timing and location of brain activity during a state of altered bodily self-consciousness by recording SEPs to stimulation of the tibial nerve of the lower leg during the FBI. SEP components to electrical stimulation (most commonly of the median nerve) have been classified as short and long latency (Allison et al., 1989a,b, 1991). Short latency components are found at 40 ms or less, and are generated in contralateral area 3b of SI. Long-latency (> 40 ms) components are thought to be generated by several areas, including, in addition to area 3b, areas 1 and 2, secondary somatosensory cortex (SII), and primary motor cortex (area 4). There have been fewer studies of SEPs to lower limb (tibial nerve) stimulation than to upper limb (median nerve) stimulation but it is known that the latency and topography of tibial nerve SEP components differs from median nerve SEPs, because of longer signal conduction times (given the greater ankle to brain than wrist to brain distance) and because of the different locations of leg and arm representation in primary somatosensory cortex (Jones and Small, 1978; Kany and Treede, 1997). Thus, for tibial stimulation the P40 component has generally been considered to be the first cortical potential (short-latency component) and is generally recorded 20–30 ms later than the first cortical potential – the N20 – to median nerve stimulation in the same participant (Kany and Treede, 1997). Like the N20, the P40 is thought to be generated in area 3b of SI (Kakigi et al., 1995), but is characterised by 'paradoxical lateralization', i.e. tibial nerve SEP amplitude is greater in the ipsilateral rather than contralateral hemisphere (Cruse et al., 1982).

For the present study, we adapted the recent SEP approach used by Dieguez et al. (2009) to the FBI setup. In order to record brain activity relevant to illusory self-identification with a virtual body we recorded SEPs in response to tibial nerve stimulation because full body representations depend on somatosensory processing from the lower limbs and because we have previously shown that self-identification and associated tactile changes (measured by the CCE) are modulated by somatosensory (proprioceptive) signals delivered to the legs but not to the wrists (Schwabe and Blanke, 2008; Palluel et al., 2011, 2012). We predicted that early activity in primary somatosensory cortex (40 ms after tibial nerve stimulation (Kakigi et al., 1982)) would reflect changes in self-identification during the FBI and, according to (Dieguez et al., 2009), that it would be enhanced during the illusion condition. We also measured the CCE during the illusion, in the same blocks as the tibial nerve stimulation, in order to test whether a change in tactile mislocalisation would also occur with the current setup, as found previously for the FBI (Aspell et al., 2009). Furthermore, this should enable us to directly compare – in the same participants and the same study – this behavioural measure of a change in tactile processing with an electrophysiological (SEP) measure.

EXPERIMENTAL PROCEDURES

Participants

A total of 18 right-handed healthy volunteers took part. All participants gave written informed consent and were compensated for their participation. The study protocol was approved by the local ethics research committee – La Commission d'éthique de la recherche Clinique de la Faculté de Biologie et de Médecine at the University of Lausanne, Switzerland and was performed in accordance with the ethical standards laid down in the Declaration of Helsinki. Data from six participants had to be discarded because they did not show an identifiable SEP (inter-participant SEP amplitude variability is known to be large (Ferri et al., 1996; Gardill and Hielscher, 2001; van de Wassenberg et al., 2008)).

Materials

The FBI was combined with a behavioural task that allowed us to assess changes in bodily self-consciousness during the illusion (CCE). For the CCE task we employed four 'light-vibration' devices, each consisting of a single bright light emitting diode (LED) paired with a small-vibrating motor (for full details see (Aspell et al., 2009)). The devices were attached to the skin using surgical tape. The two 'upper' devices were positioned at the inner edges of the shoulder blades and the two 'lower' devices 9 cm below (Fig. 1). The experiments were performed in an electrically-shielded Faraday cage. Participants were seated on