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The extrastriate body area is involved in illusory limb ownership

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ABSTRACT

The Rubber Hand Illusion (RHI) is an established paradigm for studying body ownership, and several studies have implicated premotor and temporo-parietal brain regions in its neuronal foundation. Here we used an automated setup to induce a novel multi-site version of the RHI in healthy human participants inside an MR-scanner, with a RHI and control condition that were matched in terms of synchrony of visual and tactile stimulation. Importantly, as previous research has shown that most of the ownership-related brain areas also respond to observed human actions and touch, or body parts of others, here such potential effects of the experimenter were eliminated by the automated procedure. The RHI condition induced a strong ownership illusion; we found correspondingly stronger brain activity during the RHI versus control condition in contralateral middle occipital gyrus (mOCG) and bilateral anterior insula, which have previously been related to illusory body ownership. Using independent functional localizers, we confirmed that the activity in mOCG was located within the body-part selective extrastriate body area (EBA). Crucially, activity differences in participants' peak voxels within the left EBA correlated strongly positively with their behavioral illusion scores. Thus EBA activity also reflected interindividual differences in the experienced intensity of illusory limb ownership. Moreover, psychophysiological interaction analyses (PPI) revealed that contralateral primary somatosensory cortex had stronger brain connectivity with EBA during the RHI versus control condition, while EBA was more strongly interacting with temporo-parietal multisensory regions. In sum, our findings demonstrate a direct involvement of EBA in limb ownership.

Introduction

To be oneself among others, one needs to identify with a particular body (Blanke and Metzinger, 2009; Gallagher, 2000; Jeannerod, 2007). Most accounts of body ownership have emphasized multimodal information integration in hierarchical cortical networks as a fundamental mechanism underlying a coherent self-representation (Apps and Tsakiris, 2013; Blanke, 2012; Hohwy, 2007, 2010; Petkova et al., 2011; Seth et al., 2011; Tsakiris, 2010). These theories are supported by recent neuroimaging experiments that have provided novel insights into how the brain self-attributes body parts based on such integration of visual, tactile, and proprioceptive information. In the Rubber Hand Illusion (RHI; Botvinick and Cohen, 1998), synchronous stroking of a dummy body part together with one's own corresponding body part typically misleads the brain to self-attribute the dummy limb (Botvinick and Cohen, 1998; Ehrsson et al., 2004; Tsakiris and Haggard, 2005) or even a whole body (Ehrsson, 2007; Lenggenhager et al., 2007). The experience of (illusory) body ownership has been linked to activity in frontal brain regions, predominantly the ventral premotor cortex (PMv; Ehrsson et al., 2004, 2005; Petkova et al., 2011), but also posterior regions like the right temporo-parietal junction (rTPJ; Blanke et al., 2002, 2005; Ionta et al., 2011; Tsakiris et al., 2008), posterior parietal cortex and intraparietal sulcus (PPC/IPS; Brozzoli et al., 2012; Ehrsson et al., 2004; Gentile et al., 2011; Petkova et al., 2011; Shimada et al., 2005; Tsakiris, 2010), and occipito-temporal regions like the body part-selective extrastriate body area (EBA; Arzy et al., 2006; Blanke and Mohr, 2005; Downing et al., 2001; Ionta et al., 2011). Primary somatosensory cortex (SI; Kanayama et al., 2007, 2009; Lenggenhager et al., 2011; Tsakiris et al., 2007) and the anterior insula (AI; Ehrsson et al., 2007) have also been associated with body ownership. Activity in these regions has been interpreted as reflecting the degree of illusory self-attribution or "incorporation" of the fake limb or body (Blanke, 2012; Ehrsson et al., 2004; Holmes and Spence, 2004; Petkova et al., 2011; Tsakiris, 2010).

Here, we used a fully automated setup to induce a novel, multi-site version of the RHI inside an fMRI scanner with high spatial resolution, addressing two potential caveats of the procedures typically used to evoke the illusion. First, we matched visual and tactile stimuli of both RHI and control condition in temporal synchrony, in contrast to the typically used asynchronous stroking control condition where observed touch on the dummy hand and felt touch on the own hand are presented serially. In our control condition, observed and felt touch were presented

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synchronously at spatially incongruent locations (palm and forearm). This synchronous stimulation countered potential problems associated with a serial, isolated presentation of observed and felt touch: For example, premotor cortex has been shown to be engaged in (serial) sensory predictions even in tasks using abstract, nonbiological stimuli (Schubotz and von Cramon, 2002, 2003, 2004), and the presentation of observed touch before felt touch at the same location could potentially be influenced by effects of anticipation of touch (see e.g. Carlsson et al., 2000; Keysers et al., 2010; Kuehn et al., 2012). Moreover, the resulting design enabled us to calculate a joint contrast comparing two RHI and control conditions, in which spatiotemporal differences between stimuli in the conditions were averaged out, and thus the resulting effects were attributable to the experienced illusion only. Second, by fully automating our experimental setup, we eliminated the human experimenter from the procedure. The induction of the RHI by touch from another person may interfere with self-related information processing, as many brain regions associated with body ownership (e.g., EBA, insula, PMv, and SI) also respond to observed human actions and touch, or mere vision of bodies of others (Bernhardt and Singer, 2012; Blanke, 2012; Ebisch et al., 2008; Keysers et al., 2010; Peelen and Downing, 2007; Zaki and Ochsner, 2012). Therefore, we aimed to isolate body ownership mechanisms from effects introduced by social interaction. The RHI has been induced automatically in one PET study (Tsakiris et al., 2007), but to our knowledge no automated MR-compatible RHI setup has been reported to date. We tested for BOLD signal differences between the RHI versus control condition within the ownership-related regions identified in previously published studies, expecting effects in regions whose response to the illusion is *not* influenced by receiving human touch. Moreover, we tested whether activity in those regions would reflect individual differences in the experienced intensity of the ownership illusion (Ehrsson et al., 2004; Petkova et al., 2011; Tsakiris et al., 2007).

Materials and methods

Participants

20 healthy volunteers (22–36 years old; 13 females; 19 right-handed, one classified as "mixed left-handed", measured with the Edinburgh Handedness Inventory, Oldfield, 1971; normal or corrected-to-normal vision) participated in the experiment; 16 of these participants took part in an additional scanning session for the functional EBA localizer. All participants gave written informed consent before the experiment and the study was approved by the local Ethical Committee of the Charité University Hospital (Berlin) and corresponded to the Human Subjects Guidelines of the Declaration of Helsinki.

Apparatus and procedure

A realistic life-size right dummy arm was mounted on a custom console made of transparent acrylic glass, which was set up atop the participant's chest (Fig. 1A). The participant's right arm was placed horizontally behind the dummy arm in a corresponding posture (distance between arms ~13 cm). To ensure that the location of visual stimuli in eye-centered coordinates remained the same, the participant was instructed to fixate a small dot in the middle of the dummy arm throughout the whole experiment, while her or his own arm was completely occluded from view (Fig. 1B). In contrast to previous studies (Ehrsson et al., 2004), our participants were not subjected to any prior information about the RHI and we collected the illusion intensity ratings after, not during the functional scanning sessions. For full, direct vision of the dummy arm, the participant's head was slightly tilted within the head coil (approx. 20–30°), her or his head and shoulders were foam-padded, the right arm was attached to the console with Velcro strips to eliminate motion during the experiment, and the gap between dummy arm and the participant's shoulder was covered with a black piece of cloth. Two pairs of sponge brushes were installed at anatomically corresponding locations at the palm and forearm of the own and dummy arms (Fig. 1B). Each of the brushes was separately moveable in back-and-forth 180° rotations, thereby applying touch at a specific location. To eliminate the influence of being touched by a human (seeing touch delivered with a hand may have specific effects on somatosensation; Ebisch et al., 2008; Keysers et al., 2010), and to ensure continuous temporal synchrony of strokes and corresponding stroking patterns, the brushes were driven by four separate electrical stepping motors placed outside the scanner room. The stepping motors (1.8° stepping angle; RS Components GmbH, Mörfelden-Walldorf, Germany) were controlled by a custom MATLAB (The MathWorks, Inc., Natick, USA) script via a computer parallel port, which also received the scanner-triggers to synchronize stimulation onsets with the fMRI acquisition. The motors' movements were mechanically transmitted to the brushes via a custom construction of nonmagnetic Plexiglas cables and plastic gears. During stimulation, the respective brushes performed strokes at 1.3 Hz, with random inter-stroke intervals (0, 50, or 150 ms), as an irregular stroking pattern has been shown to increase the RHI (Armel and Ramachandran, 2003). Before the start of the experiment, the two brushes touching the participant's own arm were adjusted and tested each, to assure reliable touch sensation. The participant then completed a brief practice run to get acquainted with the setup and the different stimulation types, and proceeded with the five experimental runs (see below). Subsequently, the strength of experienced ownership of the dummy arm in each condition was quantified (the

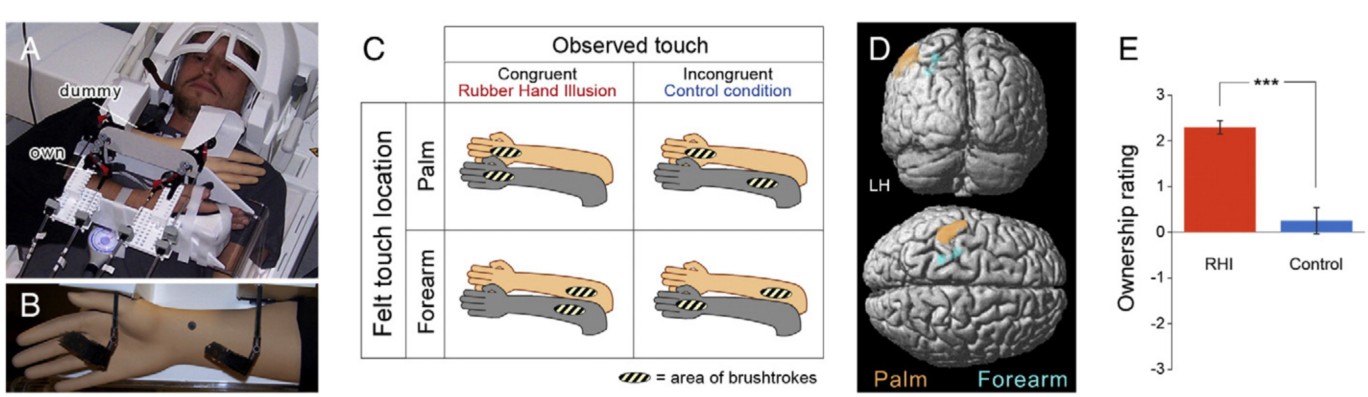

Fig. 1. (A) Experimental apparatus with the own arm occluded from view behind the dummy arm. (B) Participants' view of the dummy arm. (C) Locations of synchronous stroking on the dummy (gray) and own arm for the RHI and control condition. (D) Tactile stimulation produced significant ($p < 0.05$ FWE, small volume corrected with the left SI) activations in contralateral SI. The surface render shows the significant main effects ($p < 0.001$ uncorrected to visualize somatotopic arrangement) of stroking at the palm ($x = -48$, $y = -38$, $z = 60$, $t = 5.44$) and forearm ($x = -24$, $y = -38$, $z = 56$, $t = 3.78$) location during the visuo-tactile localizer runs, masked with anatomical left SI. (E) Participants' mean ratings of experienced ownership of the dummy arm during the RHI and control condition; error bars are standard errors of the mean, significance level obtained from Wilcoxon's signed-rank test ($z = 3.99$, $n = 20$, $p = 0.00007$).