The Neurophysiological Correlates of Illusory Hand Ownership

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Abstract

The rubber hand illusion has been established as one of the most important tools in the quest for understanding body ownership. Such understanding may be vital to neuro-rehabilitative and neurosurgical therapies that aim to modulate this phenomenon. Numerous brain imaging and TMS studies indicate that a wide ranging network of brain areas is associated with illusory hand ownership in the RHI. However, while we have a good idea of where neural activity related to the RHI occurs, the question of how these networks interact on the temporal basis is still rather unexplored as the few EEG studies that have investigated this question have relied on problematic stimulation methods or have failed to induce a strong sense of illusion in participants. Avoiding these limitations the experiments in this thesis provide insights into the temporal dynamics of body ownership in the brain.

Experiment One (presented in Chapter Three) focussed on establishing that the purpose-built, automated setup induced the Rubber Hand Illusion reliably as measured by proprioceptive drift measurements and questionnaire ratings. The evoked visual and tactile responses elicited by the setup were identified and timing and intensity of illusory hand ownership were found to be comparable to the existing literature. The results of this experiment provided guidance regarding necessary adjustments to the RHI setup for the following experiments in order to avoid confounds induced by avoidable differences between conditions.

Experiment Two (presented in Chapter Four) used a setup adjusted according to the findings of Experiment One and recorded evoked responses and oscillatory responses in participants who felt the rubber hand illusion. A combination of

experimental conditions was applied to rule out confounds of attention and body-stimulus position. In addition two control conditions were applied to reveal the neural correlates of illusory hand ownership. The experiment revealed a reduction of alpha and beta power as well as an attenuation of evoked responses around 330 ms over central electrodes associated with illusory hand ownership. Also, the results indicate that body-stimulus processing and illusion processing as measured by evoked potentials might emanate from the same cortical network.

Experiment Three (presented in Chapter Four) tested if the findings of the second experiment in regard to illusion effects were robust against changes in stimulus duration. The reduction in alpha and beta power and the attenuation of evoked responses at 330 ms were found to be robust against changes in stimulus duration. Together with the results from Experiment Two, these findings provide the first EEG marker of illusion related activity in the RHI induced by an automated setup with varying stimuli length.

Experiment four (presented in Chapter Five) investigated if the neural correlates identified in the Experiment Two and Experiment Three were indeed related to the feeling of illusory hand ownership in the RHI and not to a mere remapping of visual receptive fields. To test this, evoked and oscillatory responses were recorded during the somatic rubber hand illusion, a non-visual variant of the RHI. The somatic rubber hand illusion was found to be associated with an attenuation around 330ms post-stimulus on central electrodes, similar to the classic RHI in Experiment Two and Three. This indicated that this illusion effect in evoked responses was not related to a remapping of visual receptive fields as a result of the RHI but to the neurophysiological processes of the RHI itself.

To summarise, the results of the experiments presented in this thesis indicate that an attenuation at 330ms in evoked potentials is associated with illusory hand ownership in both, the classic RHI and the somatic RHI. Further, attenuation in alpha and beta band power is associated with illusory hand ownership in the classic RHI.

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Publications

Rao I. S., Kayser C. (2017). Neurophysiological correlates of the rubber hand illusion in late evoked and alpha/beta band activity. bioRxiv, 136846. https://doi.org/10.1101/136846

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Author’s Declaration

I declare that, except where explicit reference is made to the contribution of others, this thesis is the result of my own work and has not been submitted for any other degree at the University of Glasgow or any other institution.

Isa Rao

Definitions/Abbreviation

CCE	Crossmodal Congruency Effect
EBA	Extrastriate Body Area
EEG	Electroencephalography
EOG	Electro-oculogram
ERP	Event related potential
fMRI	Functional Magnetic Resonance Imaging
ICA	Independent component analysis
IPL	intraparietal lobe
IPS	intraparietal sulcus
LED	light-emitting diode
LOC	lateral occipital areas
PMC	Premotor Cortex
PMv	ventral premotor cortex
PPS	posterior parietal cortex
RHI	Rubber Hand Illusion
SCR	skin conductance response
TMS	Transcranial magnetic stimulation

Chapter 1: General Introduction

When we hold up our hands in front of us and look at them, we have an unambiguous feeling that these hands are ours and belong to our body. We experience this feeling of being in a body and owning this body that constitutes our physical form in daily life and rarely question it. The feeling of body ownership is an established feeling in human self-consciousness and has been pondered upon for centuries by philosophers such as Descartes and Maurice Merleau-Ponty. However, the neurophysiological processes underlying the feeling of body ownership have only recently been started to get investigated by cognitive neuroscientists.

It is important to note, that the concept of body ownership is complex and differs in its interpretation depending on the scientific or philosophical angle of observation and approach. For example, in clinical psychology, the focus lies on personality and pathological disturbances of the human consciousness, which can result in dysfunctional perception of the own body (e.g. body integrity identity disorder, eating disorders), while in the medical sciences, the term body ownership is often referred to in relation to ethical aspects of organ donation. Cognitive Neuroscientists define body ownership primarily as the sensation of experiencing a body as belonging to oneself. The studies presented in this thesis all adhere to this neuroscience specific definition of body ownership.

The Rubber Hand Illusion

One of the most important milestones in the quest of understanding body ownership has been the discovery of the so-called rubber hand illusion (RHI) by Matthew Botvinick and Jonathan Cohen (1998). Up to that point body ownership had only been investigated in clinical cases of patients suffering from somatoparaphrenia, a bodily delusion in which patients report the loss of a feeling of body ownership over one or several of their limbs after sustaining damage to the brain (Vallar and Ronchi, 2009). Allowing a departure from clinical experimental samples, the rubber hand illusion offered the possibility of investigating body ownership for the first time in healthy participants.

Botvinick and Cohen (1998) reported that healthy participants could be made to perceive an artificial hand belonging to themselves. This illusory hand ownership could be induced when a fake, but realistic, rubber hand was placed in front of the participant and the participant´s real hand was occluded from sight. Then, both the rubber hand and the participant's hand were touched in synchrony at the same location. After experiencing this stimulation for some time participants began to feel the touch as if it was originating from the place where they saw the touch on the rubber hand occurring and reported that they felt as if the rubber hand was feeling like their own hand (illusory hand ownership). In addition, participants mislocated their own hand's position towards the location of the rubber hand. The fact that this simple manipulation induced changes both in body ownership and where people felt their hand to be located, provided the means for rigorous scientific research into the factors affecting body ownership and its neurophysiological correlates.

Why should we study the Rubber Hand Illusion

The rubber hand illusion has been established as one of the most important tools in the quest for understanding the neural basis of body ownership. Such understanding could grant insights into how our brain represents our body as our own and may be vital to neuro-rehabilitative and neurosurgical therapies that aim to modulate this phenomenon. For example, Collins et al. (2017) suggested that inducing body ownership over a prosthetic hand in people who have undergone amputations could lead to improved acceptance and control over the prosthesis. As it is unlikely that continuous RHI stimulation could be provided in this case, intracranial stimulation has been suggested. So far this stimulation has focussed on bypassing the peripheral nervous system and eliciting the touch sensation directly in the brain, while at the same time providing the visual touch on the prosthesis (Collins et al., 2017). In an optimal scenario the latter step would be unnecessary as the ownership sensation over the prosthesis could be directly elicited in the brain. This however requires that we identify the neurophysiological correlates of illusory hand ownership, both in its temporal and its spatial dimension.

Besides its clinical relevance, the neural basis of body ownership is also of interest in regard to the general workings of the brain. The rubber hand illusion allows to investigate the brain's multisensory nature, tapping into visual, somatosensory and proprioceptive processing and its relationship to the ownership sensation of our body. Subsequently, the identification of the neurophysiological correlates of the rubber hand illusion bears direct relevance to the fundamental goal of cognitive neuroscience - understanding how the brain works.

Measures of the Rubber Hand Illusion

Both behavioural and subjective measures have been employed to measure illusory hand ownership in the Rubber Hand Illusion (Rohde et al., 2011). As it is not clear how well they serve as a proxy to measure intensity of feeling of illusory hand ownership in the RHI, often multiple measures are used in conjunction to determine if the Rubber Hand has successfully been induced.

Below I will outline the measurement techniques used in RHI research, while the next chapter will provide an overview of the suitability of each for measuring the intensity of feeling of illusory hand ownership in the RHI.

To capture the subjective dimension of the Rubber Hand Illusion, a range of questionnaires has been designed. Among these one of the most commonly used is the original questionnaire used by Botvinick and Cohen (1998) (Figure 1).

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○	○	○	○	○	○	○	Q1:	'It seemed as if I were feeling the touch of the paintbrush in the location where the rubber hand was touched.'
○	○	○	○	○	○	○	Q2:	'It seemed as though the touch I felt was caused by the paintbrush touching the rubber hand.'
○	○	○	○	○	○	○	Q3:	'I felt as if the rubber hand were my hand.'
○	○	○	○	○	○	○	Q4:	'It felt as if my (real) hand were drifting towards the right (towards the rubber hand).'
○	○	○	○	○	○	○	Q5:	'It seemed as if I might have more than one left hand or arm.'
○	○	○	○	○	○	○	Q6:	'It seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand.'
○	○	○	○	○	○	○	Q7:	'It felt as if my (real) hand was turning rubbery.'
○	○	○	○	○	○	○	Q8:	'It appeared (visually) as if the rubber hand were drifting towards the left (towards my own hand).'
○	○	○	○	○	○	○	Q9:	'The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other feature.'

Figure 1| The questionnaire includes the nine statements shown. Subjects indicate their response on a seven-step visual-analogue scale ranging from 'agree strongly' (+++) to 'disagree strongly' (---) (Botvinick and Cohen, 1998).

The questionnaire consists of 9 questions. Participants indicate their response on a seven-step visual analogue scale ranging from 'agree strongly' to 'disagree strongly'. The first three questions refer to experiences commonly associated with the RHI, while the last six statements serve as control for suggestibility as they describe experiences that are not commonly associated with the RHI. Other researchers have adapted these nine items to the particular focus of their studies (Longo, Schuur, Kammers, Tsakiris & Haggard, 2008; Farmer, Tajadura-Jimenez & Tsakiris, 2012; Schaefer, Konczak, Heinze, & Rotte, 2013). For example, Pavani et al. (2000) used a shortened version which only contained six questions as the focus of the studies was on the experience of the visual-tactile stimulation rather than ownership, while Kalckert and Ehrsson (2014a) added items to investigate the concept of agency in the RHI.

For capturing the behavioural dimension, the most widely applied measure is Proprioceptive drift, which measures the mislocation of one's own hand in the RHI. Proprioceptive drift is measured by noting the distance between real hand position and the indicated felt hand position before RHI stimulation and after. These scores are then subtracted and compared with the similarly derived measurement score from a control condition. Some studies additionally scale these scores in regard to arm length of the participant (Cowie et al., 2013). In participants who successfully experience the RHI the measurement score derived from the RHI condition tends to be greater than the measurement score of the control condition indicating a greater hand-localization bias. The specifics of how the distance between real hand position and the indicated felt hand position is measured differ across studies. For example, Rohde et al. (2011) projected a white dot probe into the participant's visual field onto a semi-silvered mirror while the room was darkened. The participants were instructed to move the dot probe to the felt position of their hand with the help of the scroll wheel of a mouse. Other studies (Kanayama et al., 2016; Preston, 2013; Tsakiris and Haggard, 2005) placed a ruler horizontally above the participants' hands and instructed the participants to read out the measurement from the tape that corresponded with the felt position of their index finger. This procedure was further refined by Riemer et al. (2015) who used a ruler depicting a randomized sequence of numbers from 1 to 49, interspaced by 1 cm. Participants were then asked to open their eyes and indicate which number was directly above the felt position of their own right index finger. Different rulers (depicting different number sequences) and offsets were used for each block. Most studies however rely on simply instructing their participants to close their eyes and to point at the felt location of their index or middle finger by using the index finger of their unstimulated hand (Bekrater-Bodmann et al., 2012; Botvinick and Cohen, 1998; Ehrsson et al., 2008; Fuchs et al., 2016; Kalckert and Ehrsson, 2014b; Lopez et al., 2010; Shimada et al., 2014). This pointing takes place on a measuring tape attached to either top or bottom of the tabletop where stimulation is taking place. Despite different ways of measuring proprioceptive drift across studies, the measurements are generally reported in cm and thereby allow for easy comparison. This has helped to establish proprioceptive drift as a standard technique to measure the intensity of the RHI.

Another behavioural measure of the RHI makes use of the interaction of crossmodal perception and the body. Zopf et al. (2010; 2013) developed a crossmodal congruency task in which tactile targets were presented on the real hand and visual distractors were presented on the rubber hand. Targets and distractors were spatially congruent (i.e. same finger) on some trials and incongruent (i.e. different finger) on others. Participants had to engage in a speeded forced choice location discrimination of the visual targets. The difference in performance between incongruent and congruent trials - the crossmodal congruency effect (CCE) – was found to be increased after induction of the RHI compared to a control condition.

Further, a measure using physiological changes to determine the extent of the feeling of illusory hand ownership in the RHI is the so-called skin conductance response (SCR) to threat. Armel and Ramachandran (2003) found that participants showed a higher SCR when after RHI induction the finger of the rubber hand was bent backwards. Although the manipulation affected only the rubber hand and not their real hand, participants who experienced the illusion more vividly tended to have higher SCR scores, showing a physiological response to a perceived threat. This defensive system activation has also been replicated by Ehrsson et al. (2008) and Honma et al. (2009) who found that, compared to a control condition where the illusion was not induced, stabbing the rubber hand with a needle after RHI induction led to higher SCRs among participants.

Similar to SCR in its focus on the physiological responses to the RHI, some studies monitor the temperature of the real hand that is being ‘replaced’ by the rubber hand (Moseley et al., 2008; Thakkar et al., 2011; van Stralen et al., 2013). Monitoring skin temperature in this way was based on findings by Moseley et al. (2008) who showed a relative decrease in skin temperature in the real hand of about 0.2 °C– 0.8 °C during RHI induction compared to a control condition where the illusion was not induced. The authors concluded that the illusion engages homeostatic processes in such a way that the skin temperature of the real hand decreases when participants experience ownership for the rubber hand.

It is important to note that it is not clear yet what exact aspects of the RHI some of these measures capture. For example, questionnaire data on illusory hand ownership and proprioceptive drift have been shown to be dissociated in that they capture two possibly distinct processes of the RHI. Rohde et al. (2011) compared proprioceptive drift and RHI questionnaire responses across Illusion and two control conditions. The authors found that proprioceptive drift can occur without a feeling of illusory hand ownership and that illusory hand ownership and proprioceptive drift were differently affected by both control conditions. This indicates that the processes underlying proprioceptive drift are independent of the processes that cause the feeling of ownership. Further evidence for this comes from Shimada et al. (2014) who found significant proprioceptive drift changes but no reports of illusory hand ownership after 60s of stimulation in the Illusion condition. Nonetheless, under conditions that elicit the sense of illusory hand ownership during the RHI, proprioceptive drift has been shown to correlate with the strength of this sense of illusory hand ownership (Botvinick & Cohen, 1998; Longo et al., 2008), suggesting that to an extent proprioceptive drifts can be used as a behavioural proxy of the ownership. The use of skin temperature of the real hand as a measurement of illusory hand ownership has also been debated. Skin temperature has been found to be affected by how the stimulation in the RHI is applied and thus might not be a direct correlate of the feeling of illusory hand ownership (Rohde et al., 2013a). Taken together, these findings highlight that RHI measures should be deliberately chosen in regard to the specific research question and paradigm and that measurement outcomes should be interpreted with caution.

Constraints of the RHI and the Neurocognitive Model

Two decades of behavioural research on the rubber hand illusion have revealed several factors that seem to determine if illusory hand ownership can be successfully induced. One of these was already suggested by Botvinick and Cohen (1998) who noted that temporal synchrony between the seen and felt touches was a fundamental requirement for the illusion to occur. The authors suggested that the RHI emerges from a three-way interaction between vision, touch and proprioception. Ehrsson (2012) further developed this suggestion into the “multisensory hypothesis of body ownership” which posits that illusory hand ownership and body ownership as a whole is based on the integration of concurrent body-related multisensory information (Ehrsson, 2012; Makin et al., 2008; Tsakiris, 2010).

Based on suggestions by Meredith and Stein (1986) multisensory integration is believed to follow at least two basic principles, the temporal principle and the spatial principle. These rules are essential as the brain constantly receives signals from different sensory modalities and is thereby faced with the so-called binding problem: Which of all these signals should be grouped together as containing information about the same external events and which signals are to be treated separately? Ehrsson (2012) highlights that the natural constraints of the RHI fit well with some these principles of multisensory integration (Holmes and Spence, 2005; Meredith and Stein, 1986; Stein and Stanford, 2008). For example, the temporal principle of multisensory integration states that if two sensory signals occur close to one another in time, they are likely to have been caused by the same external event. The range of temporal offsets in which this takes effect is referred to as the “temporal binding window”. In regards to the RHI, Botvinick and Cohen (1998) found that only when seen and felt touch were applied in synchrony participants would start feeling the touch on the rubber hand and a feeling of ownership over the rubber hand. Thus, only when visual and touch signals occurred close to one another in time, they were perceived as having been caused by the same external event, i.e. the stroking of the rubber hand. The necessary temporal proximity of the visual and somatosensory stimulus in the RHI was further specified in recent years. Shimada and colleagues attempted to induce the RHI with delays between visual and somatosensory stimulus of up to 600 ms in steps of 100 ms (Shimada et al., 2009). The authors found that the strength of the illusion was significantly reduced when delays were greater than 300ms as measured by RHI questionnaire and proprioceptive drift. Costantini et al. (2016) expanded on these findings by measuring their participants' individual visuo-tactile binding window and then adjusting the asynchrony between visual and somatosensory stimuli in the RHI to lie in and outside of this window. The RHI as measured by questionnaire was significantly reduced in participants as soon as the asynchrony extended beyond their individual temporal binding window. Thus, temporal constraints of the RHI seem to be strongly associated with the temporal principle of multisensory integration.

Another rule of multisensory integration refers to the location of perceived sensory signals in relation to each other, the spatial principle. It posits that two or more stimuli need to occur in approximately the same location to be attributed to the same event. Indeed, the location of the applied visual and somatosensory stimuli in the RHI has been found to impact on the strength of the feeling of illusory hand ownership. Limanowski et al. (2013) provided spatially incongruent stimulation, where visual stimulation occurred on the arm, while tactile stimulation was applied on the back of the hand (and vice versa). Thus, seen and felt touch occurred on anatomically different skin locations. The authors found that in this condition illusory hand ownership as measured by verbal ownership ratings was not induced. Similarly, Gentile et al. (2013) applied visual stimulation on the back of the hand and tactile stimulation on the forefinger (and vice versa). The strength of the RHI as measured by questionnaire and SCR was significantly reduced in these conditions compared to conditions where the stimuli where applied spatially congruent. In addition, Lloyd (2007) found that the RHI diminished with increasing distance between real and rubber hand. Notably, the author found that the rubber hand needs to be placed in distances less than 30cm in relation to the real hand to elicit a strong illusion. This distance presented a spatial limit outside of which the strength of the illusion diminished rapidly. This spatial limit suggests that the rubber hand needs to be placed within peripersonal space of the participant's real hand. While the above mentioned studies indicate that some of the spatial constraints of the RHI resemble the spatial principle of multisensory integration, there is also evidence for constraints that are not directly related to the applied multimodal stimuli but to body-related information itself (Tsakiris and Haggard, 2005).

The importance of body-related factors other than spatial distance between the real and the rubber hand was highlighted in particular by Tsakiris and Haggard (2005), who systematically examined the influence of the positioning and features of the object used to 'replace' the real hand. Results indicated that illusory hand ownership in the RHI only occurred when the object being stimulated was a rubber hand of the same laterality and located in the same anatomical position as the participant's own hand (Ehrsson, 2004; Pavani et al., 2000). No feeling of ownership could be induced for a rubber hand placed at an angle of 90º from the participant' own hand or when a rubber hand of the opposite laterality from the participant's hand was used. The importance of the position and the anatomical plausibility of the rubber hand was further underlined by Ide et al. (2013) who found that participants perceived higher ownership of the rubber hand when it was placed at an angle that was easy to mimic with the actual hand as opposed to angles that indicated anatomical incongruence. In addition, most studies find that illusory hand ownership can only be induced over a hand shaped object. (Bertamini and O'Sullivan, 2014;

Guterstam et al., 2013; Tsakiris et al., 2010, but see Guterstam et al., 2013 and Ma and Hommel, 2015). Taken together, these findings imply that beyond basic multisensory integration processes, body-related representations play a role in the RHI (Tsakiris et al., 2010).

Control conditions

To identify behavioural and neurophysiological features of illusory hand ownership in the RHI several control conditions have been developed. These control conditions tap into the bottom-up and top-down constraints described above and aim to constitute conditions in which the illusion is abolished or diminished. One commonly used control condition in studies on the RHI is the so called Asynchronous condition in which the experimenter induces an asynchrony between the felt stimulation on the participant's real hand and the seen stimulation on the rubber hand. Studies either rely on random stimulation delays between the visual and somatosensory stimuli or a constant asynchrony of e.g. 500 ms - 1000 ms (Tsakiris et al., 2007) or 2000 ms (Riemer et al., 2015b). As the asynchronous condition changes the temporality of stimulation it is generally not used for neurophysiological investigations of the RHI. Instead researchers often rely on the so called Incongruent condition in which stimuli are applied synchronously. The incongruence in the condition relates to spatial aspects of either the stimuli or the rubber hand itself. For example, Kanayama et al. (2015) applied visual and somatosensory stimulation on different fingers while Limanowski et al. (2015) provided visual stimuli on the rubber hand's palm while the somatosensory stimulation was applied on the participant's forearm (and vice versa). The spatial incongruence however can also be induced by flipping the rubber hand by 180 degrees along its longitudinal axis (Zeller et al., 2015) or placing the rubber hand at an anatomically incongruent angle (Schmalzl et al., 2014). Another control condition, the so called Real condition abolishes the illusion by removing the rubber hand from the setup. Visual and tactile stimulation now occur as one single event on the participant's real hand (Zeller et al., 2015). Further, Rohde et al. (2011) used a so-called Vision only condition in which the rubber hand was present but no stimulation was applied, neither on rubber hand nor real hand. The choice of control condition varies depending on the nature of the research. Incongruent and Real condition are often used as control conditions in studies using methods of high temporal resolution , such as EEG and MEG, as the synchronicity of stimuli is preserved, while behavioural studies often rely on the easily applied Asynchronous condition.

Neural Correlates of the RHI – The current state of knowledge

fMRI and TMS studies

Several neuroimaging studies have attempted to shed light on the neural correlates of the RHI. Using fMRI and comparing synchronous, asynchronous and incongruent conditions, Ehrsson et al. (2004), Ehrsson, Holmes, and Passingham (2005) and Ehrsson et al. (2007) concluded that neural activity in the ventral premotor cortex and posterior parietal cortex reflects the feeling of illusory hand ownership. Further evidence for this comes from (Bekrater-Bodmann et al., 2014) who compared synchronous and asynchronous conditions and found significant activation in contralateral ventral premotor cortex and intraparietal cortex. Occipito-temporal regions like the body part-selective extrastriate body area have also been implicated, e.g. by Limanowski et al. (2014) who compared spatially congruent and incongruent conditions and Limanowski & Blankenburg (2016) who applied the Illusion condition, asynchronous condition and real condition. Furthermore, studies have found activations associated with the illusion in the anterior insula (Apps et al., 2013; Guterstam et al., 2013; Limanowski et al., 2014; Petkova et al., 2011). The possible involvement in the RHI of each of these regions will be explored in the next paragraphs.

Posterior parietal regions

Converging evidence suggests that the posterior parietal cortex (PPC) is involved in mapping the position and orientation of limbs in space according to a body-centred reference (Grivaz et al., 2017). This makes this region a prime candidate for underlying the occurrence of proprioceptive drift as part of illusory hand ownership. In an fMRI study by Lloyd et al. (2003) the intraparietal sulcus (IPS) in particular showed activation for tactile stimulations of the upper limb depending on the location of the stimulated limb in space. Further, Azañón et al. (2010) found that TMS pulses over the PPC impaired the ability of remapping the spatial location of two stimuli depending on the position of the limb in space. Kammers et al. (2009) showed that repetitive transcranial magnetic stimulation over the intraparietal lobe (IPL) attenuated the strength of the RHI as measured by proprioceptive drift, while subjective self-reports of feeling of ownership over the rubber hand remained unaffected. While it is not clear yet to what extent proprioceptive drift and illusory hand ownership are associated, these findings indicate that posterior parietal regions and in particular the intraparietal regions are key areas for multisensory reference frame realignments during illusory hand ownership.

Premotor cortices

Premotor cortex and in particular the ventral premotor cortex has been implicated as a crucial region for illusory hand ownership as several studies have found that its neural activity correlates with the subjective ratings of the strength of the illusion (Ehrsson, 2004; Ehrsson et al.; Gentile et al., 2013; Petkova et al., 2011). This is further supported by the observation that human premotor lesions are associated with disorders of bodily awareness, such as anosognosia for hemiplegia (i.e. lack of awareness of motor deficits in the contralesional limbs; Berti et al., 2005) and asomatognosia (i.e. lack of awareness of parts on one's own body; Arzy et al., (2006). Similarly to the posterior parietal cortices, the premotor cortex has also been associated with body-related multisensory integration during the RHI. Makin et al. (2008) note that the premotor cortex shows additional multisensory responses compared to parietal cortices during experience of illusory hand ownership. Tsakiris (2010) suggests that this supra-additive response could be explained by the enhancement of the responses of neurons responding to somatosensory and visual stimuli once their reference frame is centred on the rubber hand and participants start referring the touch to the rubber hand as a result of binding together the visual and tactile stimuli. These findings suggest that the premotor cortex plays a substantial role in the RHI, both in regards to the feeling of illusory hand ownership and the multisensory integration processes that underlie the RHI.

Insula

Another region that has been consistently found to be activated in the RHI is the insula (Grivaz et al., 2017). Ehrsson et al. (2004) found that activity of the anterior insula covaried with behavioural and subjective measured in the RHI, while Tsakiris et al. (2007) found similar effects in the posterior insula. Increased anterior insular activity was also reported when an owned rubber hand was threatened (Ehrsson et al., 2007). Findings in clinical populations also support a major role of the insula in body ownership, as patients suffering from somatoparaphrenia (a delusion where one denies ownership of a limb or an entire side of one's body) or heautoscopy (a hallucination in which one sees one's own body from a distance) often show brain damage centering on the right insula (Cereda et al., 2002; Karnath and Baier, 2010). In addition, right insular activity has repeatedly been shown during self-attribution (Farrer and Frith, 2002) and self-processing (Vogeley et al., 2004). Taken together these findings strongly indicate that the insula is indeed a critical structure involved in illusory hand ownership.

Occipito-temporal regions

Modulated activity during illusory hand ownership has also been found in occipito-temporal regions, such as the body-part selective extrastriate body area (EBA; Limanowski et al., 2014; Limanowski and Blankenburg, 2015). Crucially, in these studies activity differences correlated strongly with participants' behavioural illusion scores indicating that EBA activity reflected interindividual differences in the experienced intensity of illusory limb ownership. Further evidence for the involvement of the EBA in illusory hand ownership comes from (Wold et al., 2014) who found that proprioceptive drift in the RHI was intensified following transcranial magnetic stimulation of the left EBA.

EEG studies

So far only a small number of EEG studies has attempted to elucidate the temporal aspects of the neural correlates of the RHI. Across these studies, illusion related changes in evoked potentials were reported both at short latencies around 55 ms on frontocentral electrodes (Zeller et al., 2015) and at much longer latencies around 460 ms on central electrodes (Peled et al., 2003). In partial agreement with previous fMRI studies on the RHI, Zeller et al. (2015)

localised the attenuation around 55 ms to the primary somatosensory cortex and the anterior intraparietal sulcus. Peled et al. (2003) suggested an involvement of the parietal cortex in the attenuation at 460 ms due to electrode location. In terms of oscillatory activity, both, a decrease in alpha and beta power (Faivre et al., 2017) and greater interelectrode synchrony in the gamma band range (Kanayama et al., 2007, 2009, 2016) have been reported.

Two models of body ownership in the RHI

The findings in fMRI and EEG studies have resulted in the formulation of two neurocognitive models of ownership in the RHI. The first model was suggested by Tsakiris (2010) and posits that the strength of illusory hand ownership over a foreign object is determined by a series of comparisons between sensory information entering the brain and various different representations of the body. In the first comparison step the shape of the object being viewed is compared with a model of the visual, anatomical and structural properties of the participant's hand/arm. This first step of testing the incorporeability of the external object is suggested to be based on processing in the right temporo-parietal junction. The second comparison is between the current postural and anatomical features of the participant's own hand/arm and those of the observed object which is ascribed to activity in the secondary somatosensory cortex. The final comparison is between the seen touch on the observed object and the felt touch on the participant's own hand which is mostly reliant on activity the posterior parietal and ventral premotor cortices, areas coding for the recalibration of the hand-centred coordinate systems (Tsakiris, 2010). According to Tsakiris (2010) the subjective experience of body-ownership resulting from the aforementioned steps is underpinned by the right posterior insula. A second model of body ownership in the RHI was suggested by Makin et al. (2008). The authors suggest that visual information about the rubber hand and proprioceptive coordinates from the real hand are conveyed to neuronal populations in posterior parietal cortex including IPS, the PMC, and the cerebellum. If the rubber hand is situated in an anatomically plausible position, the integration of sensory information is weighed heavily in favour of vision. Under these circumstances, visual stimuli presented near the rubber hand should trigger peri-hand mechanisms: the seen stimulus on the rubber hand is processed as if it was occurring close to the real hand. Subsequently, once the space around the rubber hand is represented as peri-hand space, the visual stimulus is represented in reference frames centred on and with respect to the rubber hand. At the same time, the felt somatosensory stimulus on the real hand will also activate the same bimodal mechanism. This conjunction of visual and tactile sensory information in hand-centred coordinates results in the perceived occurrence of a single visual–tactile event on the rubber hand. Makin et al. (2008) suggest that this referral of touch might be sufficient for inducing ownership over the rubber hand. The authors suggest that activity in the PMC could constitute the neurophysiological processes associated with the resulting feeling of illusory hand ownership.

Thesis rationale

fMRI and TMS studies on the RHI indicate that a wide-ranging network of brain areas is associated with illusory hand ownership. Thus, we have a good idea of where neural activity related to the RHI occurs but the question of how these networks interact on the temporal basis is still rather unexplored as only a few EEG studies have investigated illusory hand ownership (Faivre et al., 2017; Kanayama et al., 2007, 2009, 2016; Peled et al., 2003; Press et al., 2008; Zeller et al., 2015, 2016). Interpretation of the results of these studies is complicated as all have either relied on manual stimulation to induce the RHI (Faivre et al., 2017; Peled et al., 2003; Zeller et al., 2015, 2016) or have failed to induce a strong feeling of illusion in participants (Kanayama et al., 2007, 2009, 2016). Avoiding these limitations the work contained in this thesis represents the first systematic EEG investigation of illusory hand ownership using automatic stimulation. Analysis of the EEG signal in all experiments included both, event related potentials (ERPs) and a time-frequency based approach.

Thesis at a Glance

In the series of experiments presented in this thesis I sought to elucidate the neural correlates of illusory hand ownership through a combination of varying parameters within an automated RHI setup and applying EEG recordings. More specifically, I manipulated stimulus length and control conditions/comparisons within the RHI and a non-visual variant of the RHI to uncover the neurophysiological correlates of the rubber hand illusion in evoked and oscillatory activity.

In the first experiment (presented in Chapter Three), I aimed to establish that my purpose-built, automated setup induced the Rubber Hand Illusion reliably as measured by proprioceptive drift measurements and questionnaire ratings. The goal was to identify the evoked visual and tactile responses elicited by the setup and compare timing and intensity of illusory hand ownership to the existing literature. Elicited tactile and visual components were successfully identified. While the novel RHI setup induced the RHI reliably, the ERP analysis suggested that the setup had to be adjusted in terms of LED position to avoid confounds induced by avoidable differences between conditions.

In the second experiment (presented in Chapter Four), a setup adjusted according to the findings of the first experiment was used to record evoked responses and oscillatory responses in participants who felt the rubber hand illusion. I applied a combination of experimental conditions to rule out confounds of attention, body-stimulus position and stimulus duration, and relied on two control conditions to reveal the neural correlates of illusory hand ownership. The experiment revealed a reduction of alpha and beta power as well as an attenuation of evoked responses around 330 ms over central electrodes associated with illusory hand ownership.

In the third experiment (presented in Chapter Four), stimulation parameters were varied, to test if the findings of the second experiment were robust against changes in stimulus duration. The reduction in alpha and beta power and the attenuation of evoked responses at 330 ms were found to be robust against changes in stimulus duration.

Finally, the aim of experiment four (presented in Chapter Five) was to investigate if the neural correlates identified in the second experiment and third experiment were indeed related to the feeling of illusory hand ownership in the RHI or rather to a mere remapping of visual receptive fields. To test this, evoked and oscillatory responses were recorded during the somatic rubber hand illusion, a non-visual variant of the RHI. The somatic rubber hand illusion was associated with an attenuation around 330ms post-stimulus on central electrodes, similar to the classic RHI in experiment two and three. This indicates that this illusion effect in evoked responses is not merely related to a remapping of visual receptive fields as a result of the RHI but to the neurophysiological processes of the RHI itself.

Chapter 2: EEG Methods Overview

What is Electroencephalography?

Electroencephalography is a non-invasive brain imaging technique that records electrical activity from the brain with a millisecond time resolution. As neural responses are modulated by internal and external events on the order of milliseconds this makes EEG a suitable method to measure the temporal aspects of brain processes. To record EEG, electrodes are placed on multiple locations on the scalp. These electrodes can detect the electrical currents from the synchronised firing of neurons occurring in the brain. More specifically, it has been suggested that EEG reflects voltages generated (mostly) by excitatory postsynaptic potentials from apical dendrites of massively synchronised neocortical pyramidal cells (Olejniczak, 2006). While EEG allows for recording of signals from the whole brain simultaneously, valuable information from single electrodes can also be extracted. These include amplitude, latency and frequency of the electrical signal that is measured at the specific electrode location. The main limitation of EEG is its low spatial accuracy. The reason for this disadvantage is twofold. Firstly, each electrode not only records activity from the neurons directly below it but also from surrounding areas and other distributed sources in the brain. Secondly, the electrical propagation properties of the EEG signal mean that signals radiate out from the sources in varying manners depending on the orientation of the neurons and the tissue they pass through. This complicates the identification of where the EEG signal originates from and thus warrants caution in making spatial interpretations on the basis of EEG.

Event-related Potentials

ERPs are positive or negative deflections of voltage that become evident when EEG time segments time-locked to a class of repeated stimulus or response events are averaged. As a result of averaging across a large number of these time segments or epochs, it is thought that non-related, random activity in the EEG cancels out, approaching zero as the number of epochs increases. The waveforms that survive this averaging process are known as ERP components. ERP components reflect deviations from a pre-event baseline, and their peak amplitudes and latencies are thought to relate to the cognitive processes triggered by the presented stimulus.

Analysing ERPs is a widely used method to study the brain as ERPs are simple and fast to compute and have high temporal precision and accuracy. However, there are many kinds of dynamics in EEG data that do not have a representation in the ERP. Thus, to capture as much as possible of the dynamic and multidimensional space of brain processing, this thesis also included time-frequency based analyses.

Time-Frequency-Based approach

EEG activity measured from the brain fluctuates over time in rhythmic patterns. Known as “neural oscillations” two kinds of information are often examined in regards to these. Firstly, neural oscillations show variations in the speed with which they oscillate i.e. they exhibit different frequencies. This allows for a categorisation into five different bands: delta (δ, 1-4 Hz), theta (θ, 4-8 Hz), alpha (α, 8-12 Hz), beta (β, 13-30 Hz) and gamma (γ, >30Hz). In addition, information about power can be extracted. Power is the amount of energy in a given frequency band and is calculated by squaring the amplitude of the oscillation. Time-frequency analysis can help to understand how oscillatory patterns in the brain relate to different cognitive and perceptual processes and offers a way of analysing the EEG signal beyond mere ERP analysis.

Dealing with EEG noise

Mainly due to its non-invasive nature, EEG recording is highly susceptible to various forms and sources of noise. In this context “noise” refers to any external or internal signal that is not related to cognitive processing. External noise can arise from electrical devices in the vicinity of where the recording is taking place (e.g. mobile phones, computers), or faulty recording equipment (e.g broken electrodes). Internal noise may arise from eye movements, heartbeat, body movements and neural processes related to phenomena other than the experimental task/stimulation. A number of strategies are available to deal with these noise sources. Some apply during the time of recording the data, such as ensuring the participant is sitting still and is shielded from avoidable electrical noise. Others apply during the so called pre-processing step of the recorded data. Pre-processing effectively cleans the data so that it is in a fit state to be analysed. EEG data in all experiments presented in this thesis were pre-processed in a similar fashion. Firstly, pre-processing involved epoching data so that individual trials were separated. Trials with high amplitude fluctuations ($\pm 75\mu V$) were removed. In addition to this, trials with artefacts related to eye blinks or eye movements were identified using independent component analysis (ICA) and removed using both automatic and visual procedures. The general pre-processing steps applied to the data contained in this thesis will be presented in detail in the following paragraphs. However, experiment specific parameters (e.g. time window length) will be described within each experimental chapter separately.

Artefact identification based on Independent Component Analysis (ICA)

Independent component analysis is a statistical technique that uses linear decomposition to separate the EEG signal into a set of independent components. Its use as an artefact removal technique is based on two assumptions. The first assumption is that the activity recorded on the scalp during EEG is a mix of independent sources related to artefacts and brain activity. The second assumption is that these signals propagate linearly out from sources in the brain. Subsequently, if the independent sources in the data can be successfully identified using ICA, the ones related to noise can be removed.

The ICA approach includes finding a set of weights that linearly decompose the EEG signal into a set of independent components, which provide information about the time course and spatial topography of the signal. The time course can then be examined to find large amplitude fluctuations in the data which may represent noisy electrodes or eye blinks. The spatial topography of the components can be compared to typical artefact topographies to identify further noise (Li et al., 2006). The components that have been identified as artefact components in this way can then be removed. The remaining components are projected back into the scalp channels to produce artefact fee EEG data.

ICA has been shown to be a successful technique for artefact processing within EEG (Iriarte et al., 2003 ; Plöchl et al., 2012). As opposed to the commonly used arbitrarily defined cut off threshold value to detect noise, ICA can detect small modulations in the EEG signal that may be related to artefacts. It also enables researchers to retain more data for analysis as it avoids the removal of entire trials and just removes the artefact components contained in the data. In this thesis, a combination of visual inspection and three automatic procedures were used to determine which ICA components were related to artefacts.

Artefact identification via correlation with templates

For the first step of artefact rejection, templates containing typical topography patterns related to ocular-motor activity and noisy channels were created using Matlab. This was done by inserting high amplitude values (i.e. +1 or 0.4 relative to 0) over several typical artefact areas such as the centro-frontal regions (related to eye movements), the frontal regions (as in Hipp & Siegel, 2013), the temporal areas (related to muscle activity), and single electrodes (related to noisy channels). Using these templates, the correlation between the signals in each ICA component and the signals in each of these topographical template was calculated and components with high correlations (defined as >0.7) were suggested for removal. To confirm visual inspection was used.

Artefact identification via correlation with electro-oculorgram (EOG) signals

For the second step of artefact rejection time signals of highlighted components (identified by ICA) were correlated with electro-oculogram (EOG) signals. EOG signals capture the high frequency (>30Hz) EEG potentials that get elicited by muscle movements, small eye rotations, and involuntary microsaccades (Hipp and Siegel, 2013; Muthukumaraswamy, 2013). Conventional filtering and ICA often miss these, which is a particular problem if performing time-frequency analysis. The EOG signals were calculated using the eye movement signals from four electrodes placed around the eyes. These were: a vertical electro-oculogram (VEOG), a horizontal electrooculogram (HEOG), and a radial electro-oculogram (REOG) signal (Keren et al., 2010). These three EOG signals were correlated with the signals derived from ICA, and any which had high correlations (defined as >0.8) were identified as artefacts. Again, visual inspection was used to confirm.

Artefact identification via power spectrum analysis

Finally, the power spectrum of each ICA component was computed and components were removed that had a low ratio between low frequency and high frequency power (with a low ratio defined as <6). This is because EEG data follows a power law which states that EEG power is a function of frequency. In EEG data specifically the signal has smaller power magnitude at higher frequencies than the signal at the lower frequencies. By searching for components with a low ratio between low frequency power and high frequency power (i.e. little difference, which is in contrast to what would be expected), artefactual components can be identified. In this thesis, the power spectral density ratio of each ICA component was calculated and components with a ratio >6 were then checked again for correlations between the component and the artefact templates.

To summarise, in this thesis a combination of ICA, visual inspection and automatic procedures were used to remove artefact components in the EEG data as part of the pre-processing process. Further pre-processing steps and description of the analyses done can be found in each experimental chapter.

Chapter 3: Investigating a Novel Setup for the Electroencephalographic Investigation of the Rubber Hand Illusion

Introduction

For more than fifteen years, the rubber hand illusion (RHI) has offered researchers an opportunity to systematically manipulate the experience of body ownership (i.e. the subjective feeling that a body part belongs to oneself) in experimental settings. Research on the underlying neural mechanisms of the illusion, its neurophysiological correlates, however, remains inconclusive. Identifying these correlates would not only add to the current understanding of multisensory integration of bodily signals but could also be vital for the development of optimised neuro-rehabilitative interventions after the removal of a limb (Collins et al., 2017; D'Alonzo and Cipriani, 2012; Ehrsson et al., 2008). One of the challenges in researching the neurophysiological correlates of the RHI is to apply the precise, synchronous stimulation that is necessary for the induction of the illusion. Most studies rely on manual stimulation by the experimenter, either by stroking with a finger (Moseley et al., 2008; Rohde et al., 2013b), individual paintbrushes (Botvinick and Cohen, 1998; Butz et al., 2014; D'Alonzo and Cipriani, 2012; Ehrsson, 2004; Moseley et al., 2008; Olivé et al., 2015; Smit et al., 2017) or connected paintbrushes (Ehrsson, 2009; Gentile et al., 2013; Zeller et al., 2011, 2015). While all of these variants of manual stimulation have been found to induce the illusion successfully and reliably, recent research has cast doubt on the suitability of manual stimulation in studies on the neural mechanisms underlying the RHI. For example, Rohde et al. (2013) suggests that the presence of the experimenter during the experiment might constitute a confound since social or empathic factors have been found to be involved in the RHI (Asai et al., 2011). In line with this, neural responses have been shown to vary depending on whether tactile stimulation was applied by another person or by an object (Gallace, 2010). Above all, manual stimulation does not offer consistency across trials since each brushstroke can differ in timing and intensity. This variability in the sensory stimulus can be detrimental for measuring the timing and features of the respective neural activations, in particular in neuroimaging techniques with high temporal resolution such as EEG.

Automated stimulation with its comparably higher temporal precision is therefore preferable to manual stimulation. The former has been applied both, with (Bekrater-Bodmann et al., 2014; Evans and Blanke, 2013; Slater et al., 2008, 2009; Suzuki et al., 2013) and without using virtual reality devices (Kanayama et al., 2007, 2009; Limanowski and Blankenburg, 2015; Tsakiris et al., 2007). If induced with the help of virtual reality devices the rubber hand illusion is often referred to as the so-called virtual hand. In the so-called virtual hand illusion the rubber hand is replaced by a 3D virtual image of a hand, that is presented to the participants either through a head mounted display (Bekrater-Bodmann et al., 2014; Evans and Blanke, 2013; Shimada et al., 2014) or on a back-projected screen (Slater et al., 2008). Tactile stimulation of the real hand is accompanied by synchronous visual stimulation in the 3D virtual space.
The flexibility of this virtual space has enabled researchers to investigate e.g. how the RHI is affected by asymmetries in the fake limb (Kilteni et al., 2012), by replacement of the fake limb with a non-corporeal object (Ma and Hommel, 2015) and by substitution of the somatosensory stimulus with interoceptive signals (Suzuki et al., 2013). Nevertheless, despite advances in the accuracy of VR technology in recent years, ecology still poses a problem. In addition, research has highlighted neural responses to virtual reality stimuli can differ

from neural responses to real life stimuli (Aghajan et al., 2014). Also, Ijsselsteijn (2006) found that RHI induction in virtual reality and mixed reality produced a weaker illusion than RHI induction in reality, as indicated both by self-report and drift towards the rubber hand. It has also been noted that application of virtual reality in rehabilitation is limited due to its relatively high cost (Burdea, 2003).
There are also a number of RHI setups that apply automatic stimulation without the use of virtual reality (Kanayama et al., 2007, 2009; Limanowski and Blankenburg, 2015; Schütz-Bosbach et al., 2006; Tsakiris et al., 2007). For example, Limanowski et al. (2015), Schütz-Bosbach et al. (2006) and Tsakiris et al. (2007) used two motors with attached paint brushes to deliver visual and somatosensory stimulation to investigate the neurophysiological correlates of the RHI with fMRI and PET respectively. While this form of mechanical stimulation avoids the above mentioned problems it does not allow for the investigation of evoked responses as part of EEG. This is because the strokes of the paintbrushes differ in length and intensity depending on the position of the participant's finger/limb which is likely to relax and move subtly across trials. As a result the moving paintbrush is unlikely to elicit clearly distinguishable somatosensory ERP across trials as even small movements of the finger can change the area and timing of touch. In addition, the moving paintbrush does not result in clearly distinguishable visual ERPs. Since the RHI is a product of somatosensory, proprioceptive and visual information processing however, both, visual and somatosensory ERPs are a potentially important research avenue in uncovering the neurophysiological correlates of the RHI.

As Kanayama et al. (2007, 2009) have shown RHI induction through automated stimulation that leads to clearly distinguishable somatosensory and visual ERPs can be provided with the use of LEDs and vibration motors. The authors used a rubber hand that was holding a polystyrene cube with two LEDs attached to its corners. These corners were held by the thumb and index finger of the rubber hand respectively. The participant's real hand was holding a polystyrene cube with vibration motors affixed to the same locations. Visual-tactile stimulation consisted of a 300 ms LED flash on the rubber hand's forefinger and thumb accompanied by a synchronous 300 ms vibration pulse to the participant's forefinger and thumb. This synchronous automated stimulation induced the RHI as measured by post-stimulation questionnaires. The overall scores however were relatively low indicating that only a weak feeling of illusory hand ownership was induced. This might be due to the indirect stimulation, i.e. visual and tactile stimuli were associated with an object, not with the fingers themselves and the fact that the participant's hand was grasping something, i.e. it was not relaxed as in the classic RHI (Botvinick and Cohen, 1998).

Taking the above considerations into account, we decided to rely on an automated setup for RHI induction using LED and vibration motors placed directly under the rubber hand's and participant's middle finger. Our primary goal in the current experiment was to determine if our novel automated setup induced the RHI reliably as measured by proprioceptive drift scores and the RHI questionnaire. Further, we aimed to identify which somatosensory and visual components were elicited by our setup and compared evoked responses and alpha and beta power in the Illusion and Incongruent condition to probe the neurophysiological correlates of the RHI.

Materials and Methods

Participants

A total of 30 right-handed volunteers participated in this study (n=30 participants including 18 female, mean age = 22.8, years, SD = 3.4). We first ran a pilot study on all 30 participants to determine which participants were susceptible to the RHI. This involved 2 minutes of RHI induction using brushes similar to the ‘classic’ procedure used by Botvinick and Cohen (1998). After the stimulation participants filled out a standard RHI questionnaire (Botvinick and Cohen, 1998). 23 of the 30 total participants (n=23 participants including 14 female, mean age = 22.6 years, SD = 3.8) agreed or strongly agreed to the statement ‘During the last trial I felt as if the rubber hand were my hand’ and showed mean negative scores for the control statements. Out of these 23 participants 13 agreed to be included in the subsequent experiment (n=13 participants including 9 female, mean age = 22.1 years, SD = 3.3). All participants gave written informed consent before participation in this study. All protocols conducted in this study were approved by the Ethics Committee of the College of Science and Engineering of the University of Glasgow.

Experimental conditions

Participants sat on a comfortable chair in front of a one-compartment, open-ended box placed on a wooden platform. Their left arm was placed on an arm rest. Visual stimulation was delivered by a red light-emitting diode (LED; Seeedstudio, 10mm diameter) positioned 5 cm to the right of the box. Tactile stimulation was delivered by a vibration motor placed under the subject’s left middle finger (Permanent magnet coreless DC motor, Seeedstudio, 10mm diameter). Visual and tactile stimulation were controlled via Matlab and an

Arduino prototyping platform. A tape measure was attached to the underside of the table, stretching horizontally between the LED and the far edge of the open-ended box.

Each participant completed two sessions over two days. In each session one block of each of the four conditions was administered in a randomised order for each subject (Figure 2). The conditions differed in presence or absence of illusion and inclusion of visual, tactile or visuo-tactile stimulation events. Illusion condition: The participant's left hand was placed in the box with the tip of the middle finger positioned on a vibration motor. The right hand was placed at the other end of the platform in reaching distance of the keyboard. A lifelike rubber hand was positioned in an anatomically congruent orientation next to the box in a distance of 15cm to the participant's hidden left hand. The middle finger of the rubber hand was placed on an LED. Incongruent condition: The rubber hand was placed at an angle of 45˚. Besides this the setup was similar to the setup and stimulation protocol described in the Illusion condition (Ehrsson, 2004; Olivé et al., 2015; Press et al., 2008; Zeller et al., 2015, 2016). T_{only} condition: No rubber hand was present. Besides this the setup was similar to the setup described in the Illusion condition. V_{only} condition: No rubber hand was present. Besides this the setup was similar to the setup described in the Illusion condition and T_{only} conditon.

For all conditions, each block included 350 stimulation events. The stimulus duration of the tactile and/or visual events was always 100 ms with an inter-stimulus interval of 600 ms. Each block lasted approximately 4 minutes. In the Illusion and Incongruent condition participants were instructed to use their right hand to press the right arrow key on a computer keyboard when they felt the onset of the illusion and the left arrow key when they lost the feeling of the illusion. Further in the first session, we asked participants before the Illusion and Incongruent condition to close their eyes and use their right hand to indicate the felt position of the middle finger of their left hand on the tape measure attached to the underside of the table. This procedure was repeated after the stimulation. After the Illusion condition participants then filled out the RHI questionnaire (Figure 1).

Participants sat with their gaze fixed on the LED and wore ear plugs throughout the experiment to reduce the noise caused by the vibration motors.

We included the V_{only} and T_{only} condition to determine timing and location of somatosensory and visual components as induced by our setup. The Illusion condition and Incongruent were compared in order to tentatively probe the neurophysiological correlates of the RHI.

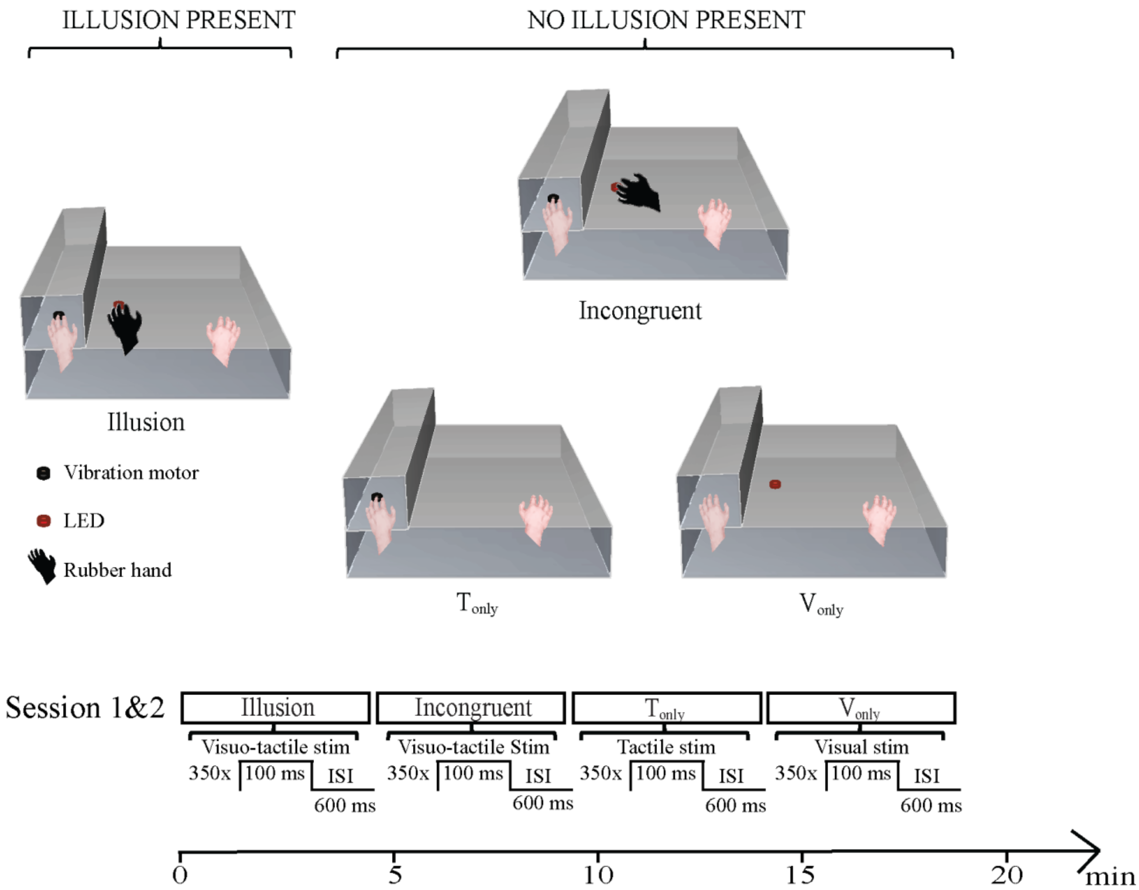


Figure 2| Stimulation and Experimental setup during the four conditions. (top panel) Illusion condition: Congruently placed rubber hand on LED, left hand on vibration motor. Incongruent condition: Incongruently placed rubber hand on LED, left hand on vibration motor. T_{only} condition: No rubber hand, no LED, left hand on vibration motor. V_{only} condition: No rubber hand, no vibration motor, left hand hidden from view. (bottom panel) Experimental setup for session 1 and 2. The order of blocks was randomised for every subject.

EEG Recording

Experiments were performed in a darkened and electrically shielded room. EEG signals were continuously recorded using an active 64 channel BioSemi (BioSemi, B.V., The Netherlands) system with Ag-AgCl electrodes mounted on an elastic cap (BioSemi) according to the 10/20 system. Four additional electrodes were placed at the outer canthi and below the eyes to obtain the electro-occulogram (EOG). Electrode offsets were kept below 25 mV. Data were acquired at a sampling rate of 500 Hz using a low pass filter of 208 Hz.

Analysis

Behavioural analysis

We computed an ownership rating score and a suggestibility score for every participant from question 1-3 and question 4-7 respectively of the administered RHI questionnaires (Figure 3). As data from the questionnaires was not normally distributed we performed a Wilcoxon signed-rank test on ownership ratings and susceptibility scores derived from the Illusion condition to ensure participants felt the illusion and that this subjective reporting was not influenced by suggestibility and task-compliance. Changes in proprioceptive drift in the Illusion and Incongruent condition were assessed by subtracting pre-stimulation scores from post-stimulation scores in each condition. The resulting proprioceptive drift score was then compared between Illusion and Incongruent condition with a Wilcoxon signed rank test as scores were not normally distributed.

EEG Analysis

Data analysis was carried out offline with MATLAB (The MathWorks Inc., Natick, MA) using the FieldTrip toolbox (Oostenveld et al., 2011). Stimulation events and their corresponding triggers were sorted based on condition, presence or absence of the illusion. For the analysis of the Illusion condition only events in which the illusion was present, as indicated by the subjects, were used. This amounted to 446 ± 93.1 (mean ± SD) for each subject. In all other conditions only events in which the illusion was absent were used. Since no occurrence of the illusion was reported in any of these conditions in the experiment, all respective events were included in the analysis. EEG data was segmented into epochs of 700 ms (200 ms pre-stimulus to 500 ms post-stimulus) and pre-processed as follows: the data were band-pass filtered between 0.5 Hz and 30

Hz, re-sampled to 200 Hz and subsequently de-noised using independent component analysis (ICA; Debener et al., 2010). We rejected trials on which the peak signal amplitude on any electrode exceeded a level of ± 75 µV, or during which potential eye movements were detected based on a threshold of 3 standard deviations above mean of the high-pass filtered EOGs using procedures suggested by Keren et al. (2010). Together these criteria led to the rejection of 34 ± 6.8 % of trials (mean ± SD). For further analysis the EEG signals were referenced to the common average reference.

Condition averages of the evoked responses (ERPs) and oscillatory power (see below) were computed by randomly sampling the same number of stimulation events from each condition. This was necessary as the number of available trials differed across conditions. Condition averages were obtained by averaging 500 times trial-averages obtained from 80% of the minimally available number of trials.

To analyse oscillatory activity we extracted single trial spectral power for alpha (8-12Hz) and beta (13-25 Hz) using a discrete Fourier transformation on sliding Hanning windows with a length of 200 ms. Power values in the range of 100 ms pre-stimulus and 350 ms post-stimulus were averaged across trials. No baseline normalization was performed but within-subject statistical comparisons were used (see below), which make the subtraction of a common baseline unnecessary. As we did not monitor eye movements we decided to not include gamma band activity in our analysis, due to its particular susceptibility to miniature saccade artifacts (Keren et al., 2010, Muthukumaraswamy, 2013).

We used spatio-temporal Cluster-based Permutation Analysis to detect significant condition differences between Illusion and Incongruent. As is standard in many similar EEG studies, a two-tailed paired t-test was performed for each electrode, and the cluster statistic was defined as the sum of the t-values of all spatially adjacent electrodes exceeding a critical value corresponding to an alpha level of 0.05, and a minimal cluster size of 2 (Kayser et al., 2015; Maris and Oostenveld, 2007). The cluster statistic was compared with the maximum cluster statistic of 2000 random permutations, based on an overall p-value of <0.05.

Results

Behavioural Results

Illusion onset occurred on average 31.3 ± 32.3 seconds (mean ± SD) after the start of stimulation onset in the Illusion blocks. No participants lost the feeling of the illusion after its initial onset. No illusion sequences were reported in any other block. Ownership ratings were significantly higher than the suggestibility scores in the Illusion blocks (Z= 3.19, p<0.01, Wilcoxon signed-rank test; Figure 3).

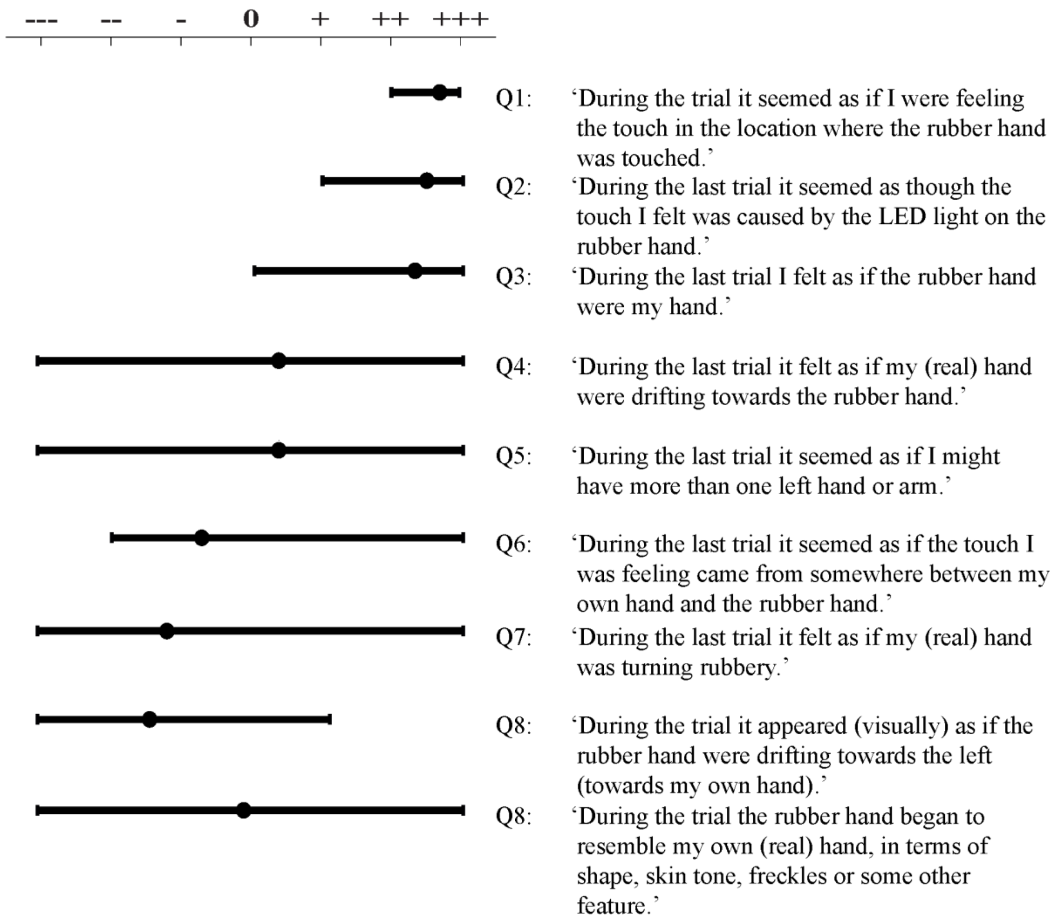


Figure 3| The questionnaire included the nine statements shown. Subjects indicated their response on a seven-step visual-analogue scale ranging from 'agree strongly' (+++) to 'disagree strongly' (---). Points indicate mean responses. Bars indicate response range.

Similarly, proprioceptive drift scores were significantly higher for the illusion condition (7.6 ± 3.5, mean ± SD) compared to the Incongruent condition (0.5 ± 0.9, mean ± SD; Z= 3.19, p<0.01, Wilcoxon signed-rank test; Figure 4).

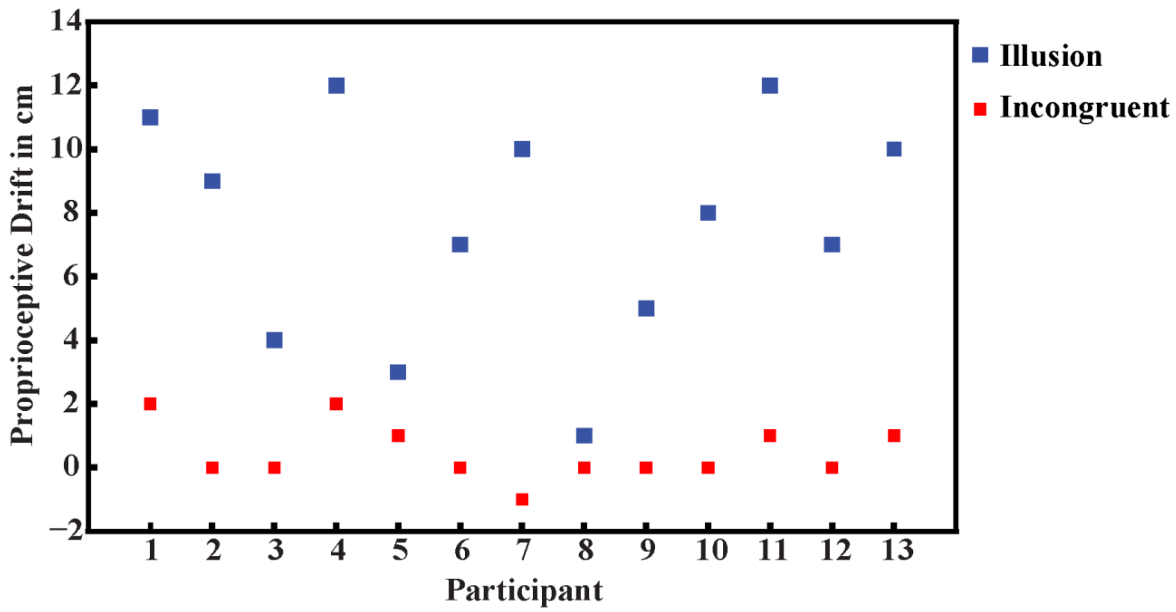


Figure 4| Proprioceptive drift (i.e. change of perceived finger position post-stimulation relative to perceived finger position pre-stimulation in cm) for Illusion and Incongruent conditions for each participant.

EEG Results

Unisensory ERPs: visual inspection

Grand averaged unisensory visual and somatosensory ERPs are shown superimposed for select electrode sites (**Error! Reference source not found.**). We visually inspected electrode sites located contralateral to the side of somatosensory stimulation (FC2) and contralateral to the side of visual stimulation (PO4) at which somatosensory and visual components are commonly found (Eimer and Forster, 2003; Hämäläinen et al., 1990; Ohara et al., 2006; Senkowski et al., 2011; Teder-Sälejärvi et al., 2002). The somatosensory N140 was clearly discernible at electrode sites around FC2 with a broad asymmetrical peak between 120 ms-150 ms post-stimulus. The visual components P1 and N1 were clearly discernable on electrodes around PO4 with peaks at around 115 ms and 155 ms respectively. Amplitude and latency of ERP amplitude peaks varied depending on electrode location.

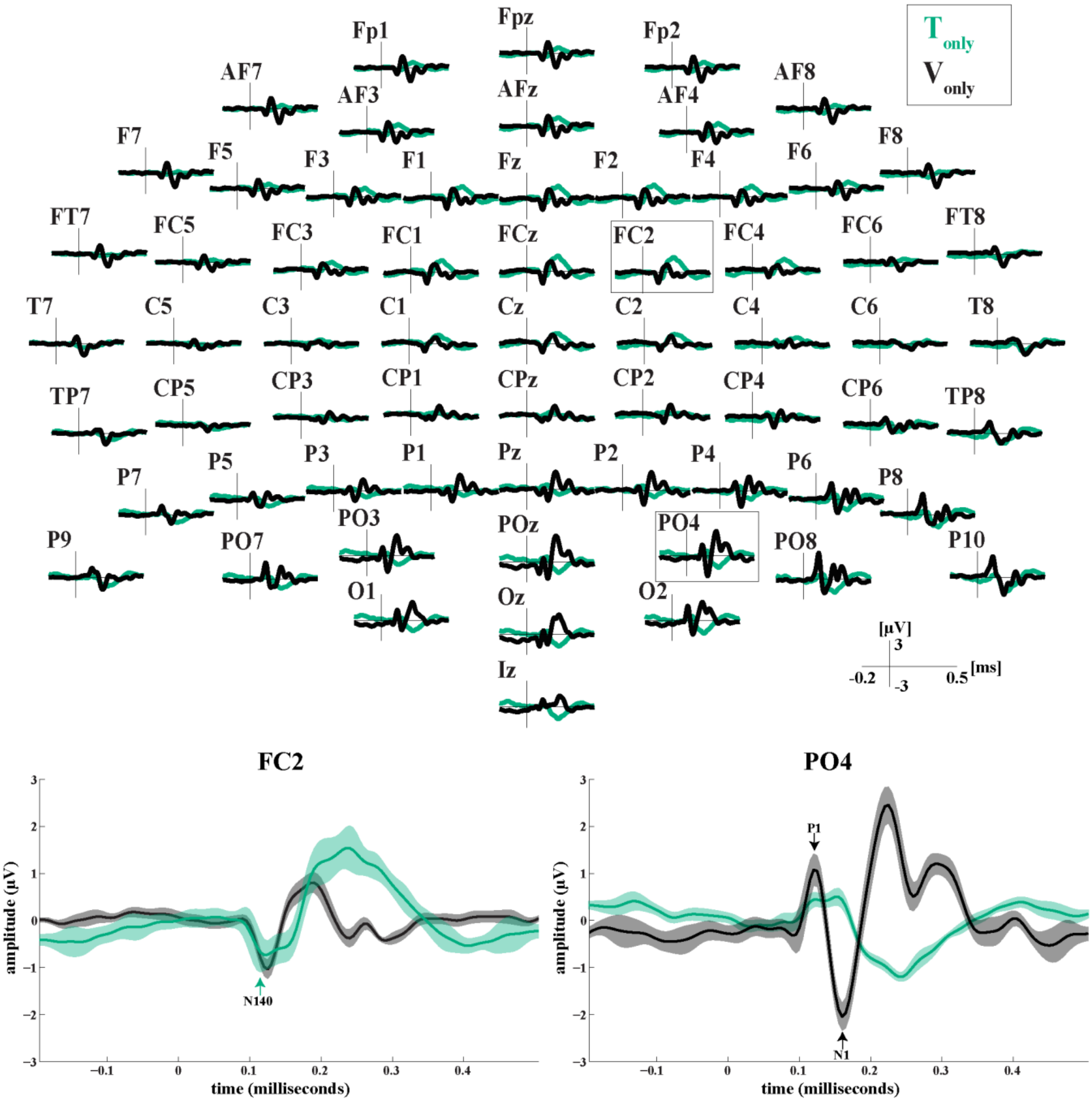


Figure 5| (top panel) Scalp distribution of evoked responses in the T_{only} condition (green) and V_{only} condition (black). (bottom panel) ERPs for T_{only} and V_{only} at electrodes FC2 and PO4.

Multisensory ERPs: visual inspection

Grand-averaged multisensory ERPs from the Illusion and Incongruent conditions are shown superimposed for select electrode sites (Figure 6). In both conditions frontal and central electrodes showed a negative peak around 120 ms and a positive peak around 185 ms post-stimulus. Electrodes over parietal and occipital areas displayed a positive peak around 115 ms and a negative peak around 155 ms post-stimulus. The negative peak at 155 ms was notably enhanced in the Incongruent condition compared to the Illusion condition.

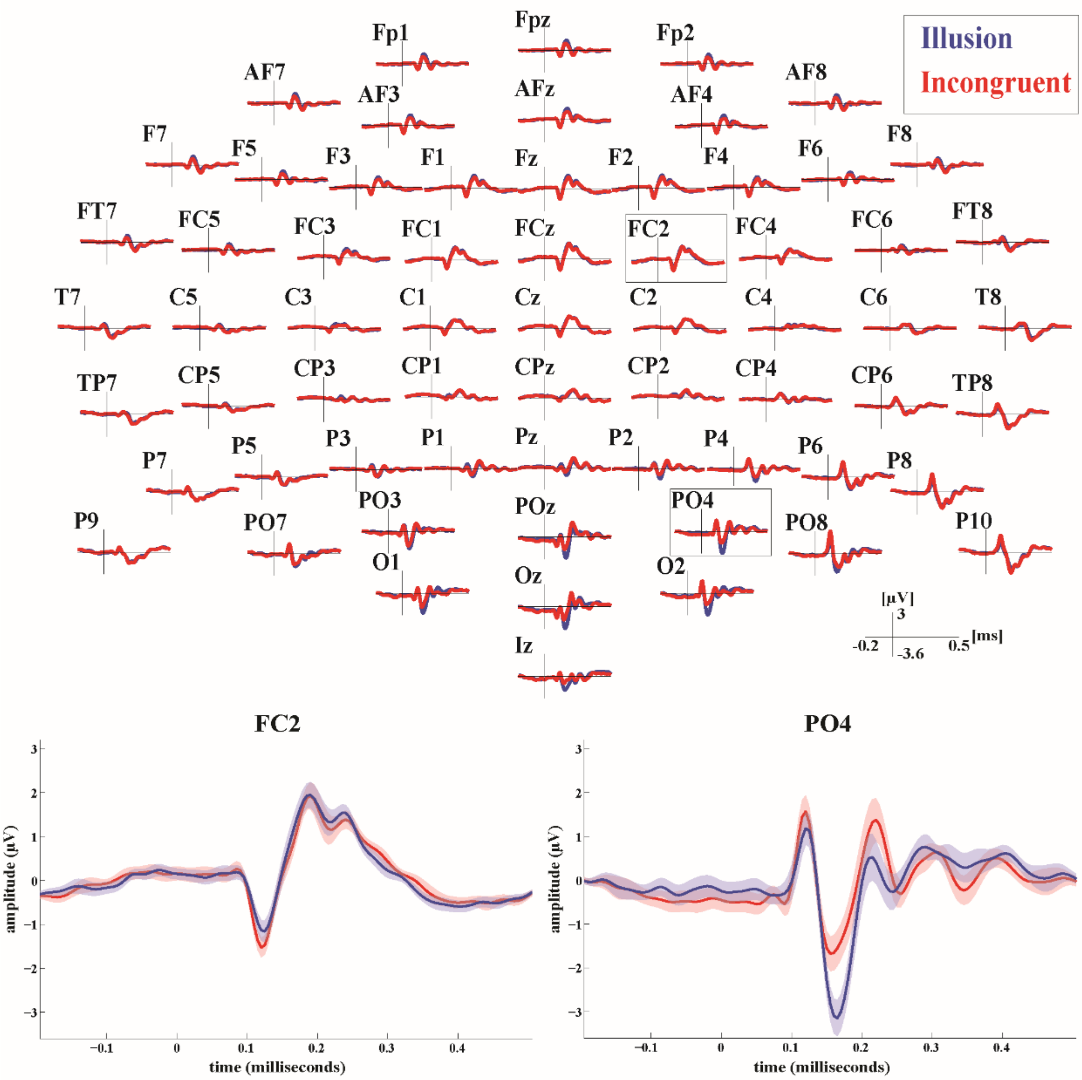


Figure 6| (top panel) Scalp distribution of evoked responses in the Illusion condition (blue) and Incongruent condition (red). (bottom panel) ERPs for Illusion and Incongruent at electrodes FC2 and PO4.

Illusion vs. Incongruent - ERPs and oscillatory activity

For ERPs, no significant differences (cluster-permutation test, at least p<0.05) were found between the Illusion condition and the Incongruent condition (Figure 6). However, on and around electrode PO4 an attenuation between 150 ms and 200 ms in the Illusion condition was visually discernible.

For oscillatory activity, no significant clusters (cluster-permutation test, at least p<0.05) were found between the Illusion condition and the Incongruent condition neither in alpha (8-12 hz) nor beta band (13-25 hz).

Discussion

In the present study we build a novel setup for induction of the RHI and investigated if this novel automated visuo-tactile setup reliably induced the illusion in our participants. Further we identified the visual and somatosensory ERP components that were elicited by our setup in unisensory, Illusion and Incongruent conditions. We found that our setup reliably induced the RHI and produced commonly identified somatosensory and visual components in the unisensory conditions. No statistically significant difference in ERPs and oscillatory activity was found between Illusion and Incongruent condition but notable differences in a late peak measured on electrodes over the visual area highlighted the need for an adjustment of LED location in future setups.

Behavioural results

Our modified automated RHI setup elicited the illusion reliably as indicated by all applied behavioural measures. Timing of onset of the feeling of ownership was on average 31.3 ± 32.3 seconds (mean ± SD) after start of stimulation. This falls into the range of onset times previously reported in studies. For example, using manual stimulation Ehrsson et al. (2007) reported that the mean time to the onset of the illusion as 11.3 ± 7.0 s (2004) and 14.3 ± 9.1 s. Slater et al. (2009) utilized virtual reality and manual stimulation and reported onset times of 43 ± 34 seconds. The onset times in the current study are most closely matched by the onset times reported by Ide et al. (2013) who relied on automated somatosensory stimulation and found that participants reported an illusory feeling of hand ownership after around 30 seconds of stimulation. This indicates that stimulation onset times are likely to vary depending on the kind of stimulation that is being applied. We can conclude that while onset times in the present study were slightly longer than those reported in studies using manual stimulation, they fall within the range of onset times reported in studies using automated stimulation.

In the current experiment, we found significantly higher proprioceptive drift in the Illusion condition compared to the Incongruent condition. The increase in drift when comparing pre-and post-stimulation scores in the Illusion condition was on average 7.6 cm. This is exceeds previous results reported, both, after manual stimulation and automated stimulation. Using manual stimulation Haan (2017) reported proprioceptive drift scores between 3.2 and 5.9 cm across five different experimental data sets. Studies using automated stimulation, generally report lower drift scores around 1.9 cm (Tsakiris et al., 2007) and 2 cm (Kanayama et al., 2016). While type of stimulation appears to play a role in the intensity of the measured proprioceptive drift, the differences between the current and previous findings is likely related to the duration of stimulation in induction of the RHI. We applied stimulation for 3.5 minutes which is substantially longer than in the above mentioned studies which relied on stimulation lasting 1.5 minutes (de Haan et al., 2017), 2 minutes (Tsakiris et al., 2007) and around 3 minutes (Kanayama et al., 2016). As it has been shown that proprioceptive drift gradually builds over time (Rohde et al., 2011), the increased proprioceptive drift score in our experiment is thus likely to be a result of our prolonged stimulation procedure. Taken together with the questionnaire results, the proprioceptive score and illusion onset time in our experiment confirm that our automated visuo-tactile setup elicits the illusion reliably and in a fashion that is comparable to previous experiments.

Neurophysiological results

The visual inspection of evoked responses in the unisensory conditions confirmed that our setup successfully elicited common somatosensory and visual components. Somatosensory stimulation led to a clearly discernible N140 around 135 ms on contralateral frontocentral electrodes. This matches descriptions of the somatosensory N140 component in the literature both in timing and location. Further, we identified the visual components P1 and N1 on contralateral parieto-occipital electrodes when visual stimulation was applied. Again, the location and timing of these components match descriptions of the visual P1 and N1 in the literature. Thus, visual and somatosensory stimulation in our setup successfully elicited commonly expected visual and somatosensory ERP components.

Analysis of Illusion and Incongruent condition did not reveal any differences in neither evoked responses nor oscillatory activity. However, our study was based on a sample size of only 13 subjects which is considered very small for neuroimaging studies (Poldrack et al., 2017). The resulting lack in statistical power has rendered our neurophysiological analysis prone to type 2 errors and undermines the found null result. Future experiments should include at least a minimum sample size of 20 participants as recommended in recent neuroimaging literature (Poldrack et al., 2017; Simmons et al., 2011).

Nevertheless, visual inspection of the evoked responses in the Illusion and Incongruent conditions revealed a greater negative amplitude on the visual N1 component in the Incongruent condition. As the visual N1 has been shown to increase in amplitude with higher stimulus luminance (Johannes et al., 1995) this difference between Illusion and Incongruent condition is possibly related to a difference in luminance of the visual stimulus between the two conditions. Indeed, closer inspections of the setup reveals that the adjustment of the rubber hand in the Incongruent condition decreases the space of the LED covered in relation to the participants eye line. As a result, stimulus luminance is increased in the Incongruent condition compared to the Illusion condition. To avoid this confound in future experiments the setup should be adjusted to keep the LED fully visible in both conditions.

Conclusions

The present experiment confirmed that our novel automated RHI setup induced the RHI reliably. In addition, we found that the setup elicited the somatosensory N140 and the visual N1 and P1 components. This underlines the suitability of our setup for investigating the neurophysiological correlates of the RHI. However, the current results also indicate that future experiments should adjust the position of the LED and rely on greater sample sizes to increase statistical power.

Chapter 4: Neurophysiological Correlates of the Rubber Hand Illusion in late Evoked and Alpha/Beta Band Activity

Introduction

Philosophy, psychology, and neuroscience continue to debate the sources and modulators of conscious experience. The scientific study of consciousness has long been focussed on the visual domain, but recent decades have seen a rise of interest in bodily self-consciousness and the integration of bodily signals with other multisensory information (Jeannerod, 2007). Bodily self-consciousness refers to the integrated, pre-reflexive experience of being a self in a body and has been related to tactile, vestibular, proprioceptive, as well as visual and motor information (Blanke, 2012; Tsakiris and Haggard, 2005). One extensively investigated aspect of bodily self-consciousness is the experience that our body and its parts belong to us and are distinguished from non-body objects and other people's bodies, so-called body ownership. A widely used paradigm to study body ownership is the rubber hand illusion (RHI; Botvinick, 2004) during which participants watch an artificial rubber hand being stroked in synchrony with strokes on their own occluded hand. This synchronous visuo-tactile stimulation alters bodily experience as it induces the illusion that the rubber hand is one's own hand.

Several functional magnetic resonance imaging (fMRI) studies have aimed to identify the neural correlates of illusory hand ownership. The experience of illusory hand ownership has been linked to activity in frontal brain regions, such as the premotor cortex (Bekrater-Bodmann et al., 2014; Ehrsson, 2004; Petkova et al., 2011), occipito-temporal regions such as the extrastriate body area (Limanowski et al., 2014), intraparietal areas (Petkova et al., 2011), the anterior insula (Limanowski et al., 2014), and the temporoparietal junction (Guterstam et al., 2013). However, given the nature of the fMRI signal, these studies have not been able to provide a functionally specific picture that assigns these neural correlates to a specific part of the sensory-perceptual cascade, for example by assigning the relevant neural activations to a specific latency following each repeat of the visuo-tactile stimulation.

Overcoming these limitations, several EEG studies have aimed to reveal the physiological correlates of illusory hand ownership at higher temporal precision. One such study has described the relative attenuation of somatosensory-evoked responses during the Illusion about 55 ms after stimulus onset (Zeller et al., 2015). This attenuation was localized to the primary somatosensory cortex and the anterior intraparietal sulcus, and was interpreted by the authors as an attenuated precision of the relevant proprioceptive representations involved in the RHI. However, another EEG study using a similar experimental paradigm reported illusion-related changes in ERPs only at much longer latencies of around 460 ms over central electrodes (Peled et al., 2003). Furthermore, studies on oscillatory power showed a decrease in frontal-parietal alpha power and fronto-parietal beta power to be associated with illusory hand ownership (Faivre et al., 2016). This was interpreted as reflecting increased activation in sensorimotor cortices due to the illusion. Further support for a role of alpha band activity was provided by Lenggenhager et al. (2011) who reported a correlation between alpha band oscillations and a measure of illusory body ownership. In contrast to this, Kanayama (2007; 2009) only found greater interelectrode phase synchrony in the gamma band range (40-50 Hz) to be correlated with the perceived intensity of illusory hand ownership. Overall, it remains unclear whether neural correlates of the RHI include aspects of early sensory encoding, hence at shorter latencies relative to stimulus onset, or mostly involve higher cognitive processes emerging at longer latencies relative to the touch stimulus.

The lack of clear insights from the existing EEG studies on the RHI may in part result from the use of distinct control conditions and different stimulation parameters, and confounding factors that may have emerged as a consequence of this. Two widely used control conditions for the rubber hand illusion are the Incongruent condition, in which the rubber hand is placed at an anatomically incongruent angle, and the Real condition, in which the rubber hand is absent and stimulation occurs on the real hand in view (Ehrsson, 2004; Olivé et al., 2015; Schmalzl et al., 2014; Tsakiris et al., 2007; Zeller et al., 2015, 2016). Unfortunately, these control conditions carry inherent confounds by differing from the illusion condition by more than just the absence of the illusion. In the Real condition, the hand position is changed and the rubber hand is completely absent from the setup, hence all seen potential body parts are indeed a natural part of the participant's body. In the Incongruent condition the visual stimulation of the Rubber Hand and the somatosensory stimulation on the real hand occur in two different locations, while in the Illusion condition these stimulations are perceived to occur on one location, i.e. on the rubber hand. It is hence possible that spatial attention in the Illusion condition is focused on one location, while in the Incongruent condition attention is divided across two locations. As a result, changes in spatial attention may confound some of the previous results. In addition, in the Illusion condition, the visual stimulus is perceived to occur on the participant's body, i.e. the embodied rubber hand. The visual stimulus in the Incongruent condition however is perceived to occur not on the body, but on the non-embodied rubber hand. Previous studies have suggested that visual stimuli are processed differently when the stimuli is placed near the hand, rather than when it is not (Langerak et al., 2013). Thus, visual processing due to body-stimulus position between Illusion and Incongruent condition may differ substantially. As a result, it remains unclear whether illusion-related effects reported in previous studies are indeed only related to the illusory body experience, or rather originate from confounding factors introduced by the control conditions, such as changes in attention or body-stimulus position. We here directly investigated the role of these confounding factors by including manipulations of these in our experimental design (Experiment 3).

Differing stimulation parameters in regard to stimulus duration might have added to the discrepancy among results. Peled et al. (2003), Zeller et al. (2015) and Faivre et al. (2016) relied on manual stimulation applied by an experimenter, with inconsistent and unspecified stimulus duration, while Kanayama et al. (2007, 2009) administered automated visuo-tactile stimuli of 300ms duration. The differing stimuli durations across studies pose a problem for the identification of evoked responses related to the RHI. The use of a fixed stimulation duration as in Kanayama et al. limits the scope of the results in that the location and latency of the identified modulation related to the RHI might be specific to the respective stimulus duration. Varying and undetermined stimulus durations across trials as used by Zeller et al. and Peled et al. are problematic due to the differences in stimulus offset times and their possible influence on shape and amplitudes of evoked responses (Spackman et al., 2006; Woodman, 2010). For these reasons, it remains very difficult to collate findings across studies and to reliably identify the electrophysiological correlates of illusionary hand ownership. To overcome this problem we relied on a temporally precise stimulation setup and explicitly manipulated the duration of the individual stimulation events (Experiment 3).

All in all, our goal was to study the neural correlates of the RHI in electroencephalographic brain activity by refining the typical protocol used to induce the RHI in three ways: First, by introducing a temporally precise stimulation apparatus that allows the recording of evoked activity that is precisely-time locked to the somatosensory and visual stimuli; second, by comparing neural correlates of the RHI across different control conditions to rule out confounds of attention and body-stimulus position; and third, by testing if the identified neural correlates of the RHI are robust against changes in stimulus duration. Given that previous studies have reported illusion-related effects both in evoked responses (Peled et al., 2003; Zeller et al., 2015) and in induced oscillatory activity (Faivre et al., 2017; Kanayama et al., 2007, 2009), we here focused on both these markers of neural processing. In the first experiment presented in this chapter we recorded EEG activity during the Illusion, the Real and Incongruent control conditions and two further conditions which varied in attention focus and body-stimulus position. We identified neurophysiological correlates of illusionary hand ownership that were consistent across both control conditions and then differentiated these from the two confounds by comparing the respective contrasts. In the second experiment, we expected to replicate these neurophysiological correlates of illusionary hand ownership, and hypothesized that these were robust against changes in stimulus duration.

Materials and Methods

Participants

A total of 52 right-handed volunteers participated in this study. We first ran a pilot study on all 52 participants, which involved 2 minutes of synchronous visuo-tactile stimulation identical to the Illusion condition described below. After the stimulation participants filled out a standard RHI questionnaire (Botvinick and Cohen, 1998). 32 of the 52 total participants agreed or strongly agreed to the statement 'During the last trial I felt as if the rubber hand were my hand' (Botvinick and Cohen, 1998) and showed mean negative scores for the control statements. Only the 32 participants who showed this response pattern were included in the subsequent two experiments, with 8 participants participating in both experiments. Thus, the presented data is from 20 participants each (Experiment 2: n=20 participants including 13 female, mean age = 23.1 years, SD = 3.1; Experiment 3: n=20 participants including 13 female, mean age = 22.1 years, SD = 2.9 years). All participants gave written informed consent before participation in this study. All protocols conducted in this study were approved by the Ethics Committee of the College of Science and Engineering of the University of Glasgow.

Experimental conditions

Participants sat on a comfortable chair in front of a one-compartment, open-ended box placed on a two-storey wooden platform. Their left arm was placed on an arm rest. Visual stimulation was delivered by a red light-emitting diode (LED; Seeedstudio, 10mm diameter) positioned 5 cm to the right of the box on the top storey. Tactile stimulation was delivered by a vibration motor placed close to the subject's skin (Permanent magnet coreless DC motor, Seeedstudio, 10mm diameter). Visual and tactile stimulation were controlled via Matlab and an Arduino prototyping platform.

In experiment 2 five conditions were administered in a randomised order for each subject (Figure 7A). The conditions differed in presence or absence of illusion, body-stimulus position (visual stimulus on body, visual stimulus not on body) and attention (focussed, divided). Illusion condition: The participant's left hand was placed in the box with the tip of the middle finger positioned on a vibration motor. The right hand was placed at the other end of the platform in reaching distance of the keyboard. A lifelike rubber hand was positioned in an anatomically congruent orientation next to the box in a distance of 15cm to the participant's hidden left hand. The middle finger of the rubber hand was placed on a dummy vibration motor. The LED was positioned five millimetres above the dummy motor. This condition is typically used to induce the RHI. Incongruent condition: The rubber hand was placed at an angle of 45˚. Besides this the setup was similar to the setup described in Illusion (Ehrsson, 2004; Olivé et al., 2015; Press et al., 2008; Zeller et al., 2015, 2016). Real condition: No rubber hand was present. The middle finger of the left hand was placed in view on a vibration motor positioned 5 millimetres below the LED. The right hand was in the same position as in the Illusion and Incongruent conditions (Zeller et al., 2015, 2016). Hand under condition: The participant's left hand was placed on the lower storey of the platform with the middle finger placed on a vibration motor. The vibration motor was positioned right below the dummy vibration motor on the top storey. The vertical distance between the two motors was 10 cm. Besides this, the setting was identical to the Incongruent condition. Two hands condition: No rubber hand was present. The middle finger of the participant's right hand was placed on a dummy vibration motor below the LED. Besides this, the setting was identical to the Incongruent condition. Throughout all conditions view of the left arm, and the trunk of the rubber hand where applicable, was obstructed by an opaque piece of fabric.

For subsequent analysis the differences in hand and stimuli location across conditions allow for a grouping of Incongruent, Real, Hand under and Two hands in regard to attentional and body- stimulus related processing (Figure 7B). In the Incongruent and Two hands conditions attention is divided, since in both conditions visual and somatosensory stimuli occur at distant locations. In the Real and Hand under conditions attention is focused, since visual and somatosensory stimuli occur at the same location. For body-stimulus related processing, Incongruent and Hand under can be grouped as the visual stimulus does not occur on the subject's body, while the Real and Two hands conditions can be grouped as the visual stimulus does occur on the participant's body.

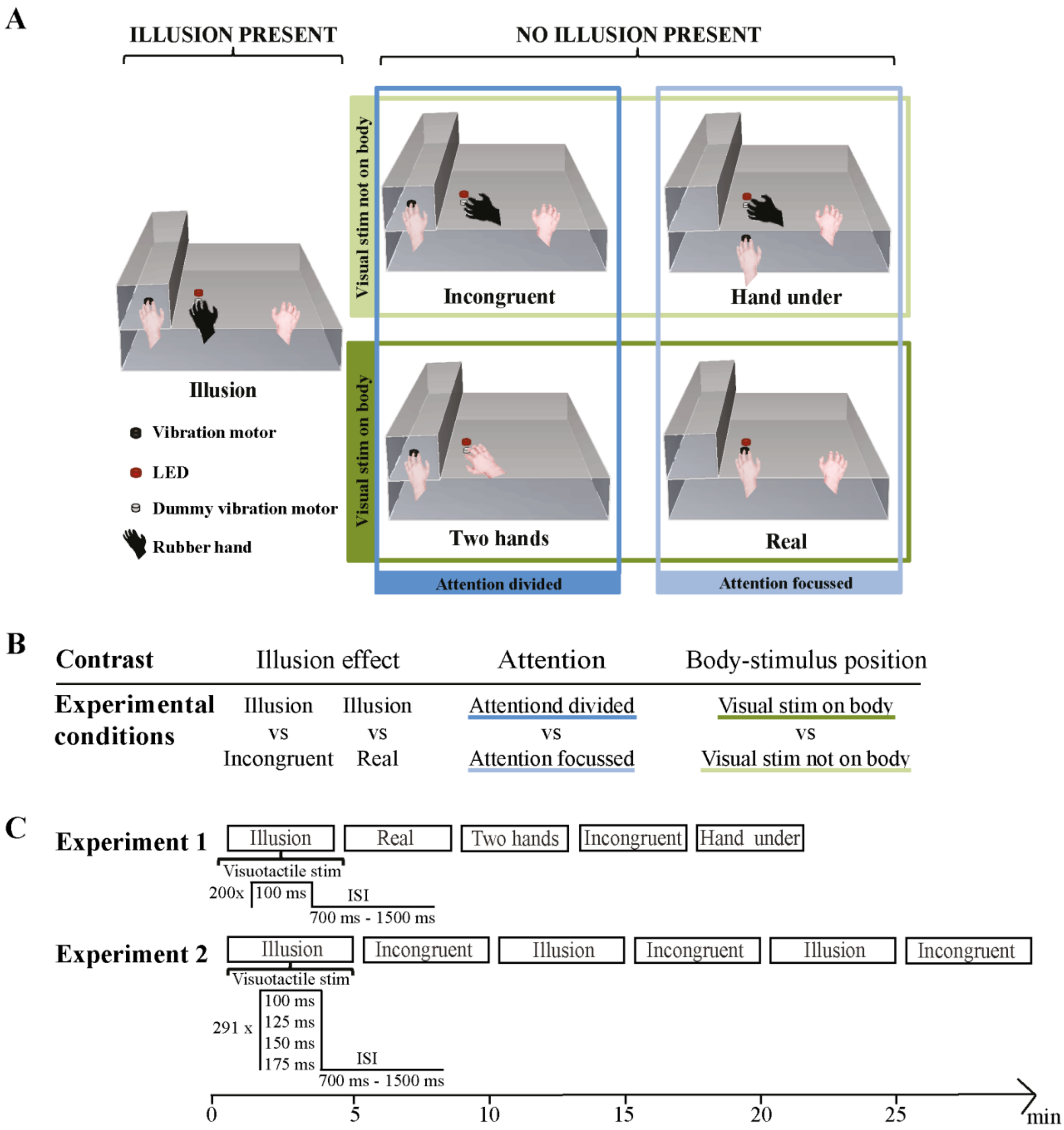


Figure 7| (A) Stimulation setup during the five conditions. Illusion condition: Congruently placed rubber hand on dummy vibration motor below LED, left hand on vibration motor. Incongruent condition: Incongruently placed rubber hand on dummy vibration motor below LED, left hand on vibration motor. Hand under condition: Incongruently placed rubber hand on dummy vibration motor below LED, left hand on vibration motor below dummy vibration motor and LED. Two hands condition: No rubber hand, left hand on vibration motor, right hand on dummy vibration below LED. Real condition: No rubber hand, left hand on vibration motor under LED. The four non-illusion conditions were additionally grouped in a 2x2 design according to the factors attention and body-stimulus position. (B) Experiment 2: Illusion effect, Attention and Body-stimulus position contrasts and the experimental conditions they are based on. (C) Experimental setup in experiment 3

(top panel) and in experiment 3 (bottom panel). The order of blocks was randomised for every subject.

Experimental procedure

In Experiment 2 one block of each condition was administered. Each block included 200 stimulation events. The visuo-tactile stimulus duration was 100 ms and the inter-stimulus interval varied randomly and evenly between 700 ms and 1500 ms. Each block lasted approximately 3.5 minutes. Experiment 3 contained three blocks of each, the Illusion and Incongruent condition administered in a pseudorandom order. Each block included 291 stimulation events. On a given stimulation event visuo-tactile stimulus duration was either 100 ms, 125 ms, 150 ms or 175 ms (pseudo-randomly assigned). Every block contained at least 64 events of each stimulus duration. The inter-stimulus interval varied randomly and evenly between 700 ms and 1500 ms. Each block lasted approximately 5 minutes (Figure 7C).

In both experiments participants were instructed to use their right hand to press the right arrow key on a computer keyboard when they felt the onset of the illusion and the left arrow key when they lost the feeling of the illusion. Participants sat with their gaze fixed on the LED and wore ear plugs throughout the experiment to reduce the noise caused by the vibration motors.

EEG Recording

Experiments were performed in a darkened and electrically shielded room. EEG signals were continuously recorded using an active 64 channel BioSemi (BioSemi, B.V., The Netherlands) system with Ag-AgCl electrodes mounted on an elastic cap (BioSemi) according to the 10/20 system. Four additional electrodes were placed at the outer canthi and below the eyes to obtain the electro-occulogram

(EOG). Electrode offsets were kept below 25 mV. Data were acquired at a sampling rate of 500 Hz using a low pass filter of 208 Hz.

EEG analysis

Data analysis was carried out offline with MATLAB (The MathWorks Inc., Natick, MA) using the FieldTrip toolbox (Oostenveld et al., 2011). Stimulation events and their corresponding triggers were sorted based on condition, presence or absence of the illusion and stimulus length (Experiment 3 only). For the analysis of the Illusion condition only events in which the illusion was present, as indicated by the subjects, were used. This amounted to 163±29 (mean±SD) events in experiment 2, and 248±34 (mean±SD) events in experiment 3. For analysis of all other conditions only events in which the illusion was absent were used. Since no occurrence of the illusion was reported in any of these conditions in either experiment, all respective events were included in the analysis. EEG data was segmented into epochs of 700 ms (200 ms pre-stimulus to 500 ms post-stimulus) and pre-processed as follows: the data were band-pass filtered between 0.5 Hz and 30 Hz, re-sampled to 200 Hz and subsequently de-noised using independent component analysis (ICA; Debener et al., 2010). To detect potential artefacts pertaining to remaining blinks or eye movements we computed horizontal, vertical and radial EOG signals following established procedures (Hipp and Siegel, 2013; Keren et al., 2010). We rejected trials on which the peak signal amplitude on any electrode exceeded a level of ±75 μV, or during which potential eye movements were detected based on a threshold of 3 standard deviations above mean of the high-pass filtered EOGs using procedures suggested by Keren et al. (2010). Together these criteria led to the rejection of 34±8 % of trials (mean±SD) in Experiment 2 and of 25±11% of trials (mean±SD) of trials in Experiment 3. For further analysis the EEG signals were referenced to the common average reference.

Condition averages of the evoked responses (ERPs) and oscillatory power (see below) were computed by randomly sampling the same number of stimulation events from each condition. This was necessary as the number of available trials differed across conditions. Condition averages were obtained by averaging 500 times trial-averages obtained from 80% of the minimally available number of trials.

To analyse oscillatory activity, we extracted single trial spectral power for alpha (8-12Hz) and beta (13-25 Hz) using a discrete Fourier transformation on sliding Hanning windows with a length of 200 ms. Power values in the range of 100 ms pre-stimulus and 350 ms post-stimulus were averaged across trials. No baseline normalization was performed but within-subject statistical comparisons were used (see below), which make the subtraction of a common baseline unnecessary. As we did not monitor eye movements we decided to not include gamma band activity in our analysis, due to their particular susceptibility to miniature saccade artefacts (Keren et al., 2010, Muthukumaraswamy, 2013).

In experiment 2 our primary aims were to determine ERP and oscillatory signatures of the illusion and to compare these to ERP and time-frequency signatures of attentional and body-stimulus position related processes. While we expected to find significant differences in evoked activity between Illusion and control conditions over parietal and centrofrontal areas (Peled et al., 2003; Zeller et al., 2015) our stimulation parametres and experimental setup differed from previous studies to such an extent that we decided to employ an unbiased approach and to test for statistical effects across all electrodes and a wide time range. We hence used spatio-temporal Cluster-based Permutation Analysis to detect significant condition differences. As is standard in many similar EEG studies, a two-tailed paired t-test was performed for each electrode, and the cluster statistic was defined as the sum of the t-values of all spatially adjacent electrodes exceeding a critical value corresponding to an alpha level of 0.05, and a minimal cluster size of 2 (Kayser et al., 2015; Maris and Oostenveld, 2007). The cluster statistic was compared with the maximum cluster statistic of 2000 random permutations, based on an overall p-value of 0.05. To identify illusion effects we compared Illusion vs. Incongruent and Illusion vs. Real conditions. For obtaining Body-stimulus position and Attention contrasts we used the four conditions Incongruent, Hand under, Two hands, Real, which differed along the factors of Attention (focussed, divided) and Body-stimulus position (visual stimulus on body, visual stimulus not on body) in a 2x2 design (Figure 7B). To obtain the contrasts for each factor we averaged over the respective conditions belonging to each level and then compared the averages with a cluster permutation test. To calculate the interaction of Attention and Body-stimulus position factors, that is the difference between the differences between the means of one factor, across the levels of the other factor, we subtracted Two hands from Real, and Incongruent from Hand under, and compared these differences with a cluster permutation test.

In experiment 3 our primary aims were to replicate the illusion effect from experiment 2 and to investigate if stimulus duration modulates this effect. For the analysis of evoked responses we selected the time point with the biggest overlap of significant electrodes between Illusion vs. Incongruent and Illusion vs. Real contrasts as found in experiment 2. We conducted a 2x4 repeated measures ANOVA with the factors illusion presence and stimulus duration on data averaged over the significant electrodes at this time point. For the analysis of oscillatory power we selected the electrodes in the overlap of significant electrodes between Illusion vs. Incongruent and Illusion vs. Real time-frequency contrasts in alpha and beta band as found in experiment 2. We conducted a 2x4 repeated measures ANOVA on power in each band. Greenhouse–Geisser correction was applied where sphericity was violated.

Results

Experiment 2

Behavioural data

Illusion onset occurred on average 41.3±32.3 seconds (mean ±SD) after the start of stimulation onset in the Illusion block. Four participants lost the feeling of the illusion after its initial onset. The resulting non-illusion sequences lasted on average 41.8 ± 29.4 seconds (mean ±SD). No illusion sequences were reported in any other block.

Illusion effect - ERPs

Significant differences (cluster-permutation test, at least $p<0.05$) between the Illusion condition and the Incongruent condition emerged around two time points: At 120 ms the Illusion condition showed lower amplitudes in right frontal regions (Tsum = -659.0, $p<0.05$) and more positive amplitudes in left parietal areas (Tsum = 490.9, $p<0.05$) compared to the Incongruent condition (Figure 8A). At 330 ms the Illusion condition showed lower amplitudes in frontocentral regions compared to the Incongruent condition and this frontocentral negativity was centred around electrode FCz (Tsum = -404.4, $p<0.05$, Figure 8A). Significant differences between the Illusion condition and the Real condition emerged around 330ms and were also centred around electrode FCz (Tsum = -

823.1, $p<0.05$; Figure 8B). The respective ERPs at electrode FCz suggest that the illusion is characterized by a more pronounced negativity of the evoked activity around 330ms in compared to the two control conditions (Figure 8C).

To better localize the illusion effect we determined those electrodes that were part of both significant effects around 330 ms, i.e. which were part of the significant time-electrode clusters in both, the Illusion-Incongruent and Illusion-Real contrast. The resulting electrodes comprised the medial central and centrofrontal electrodes (Figure 8D).

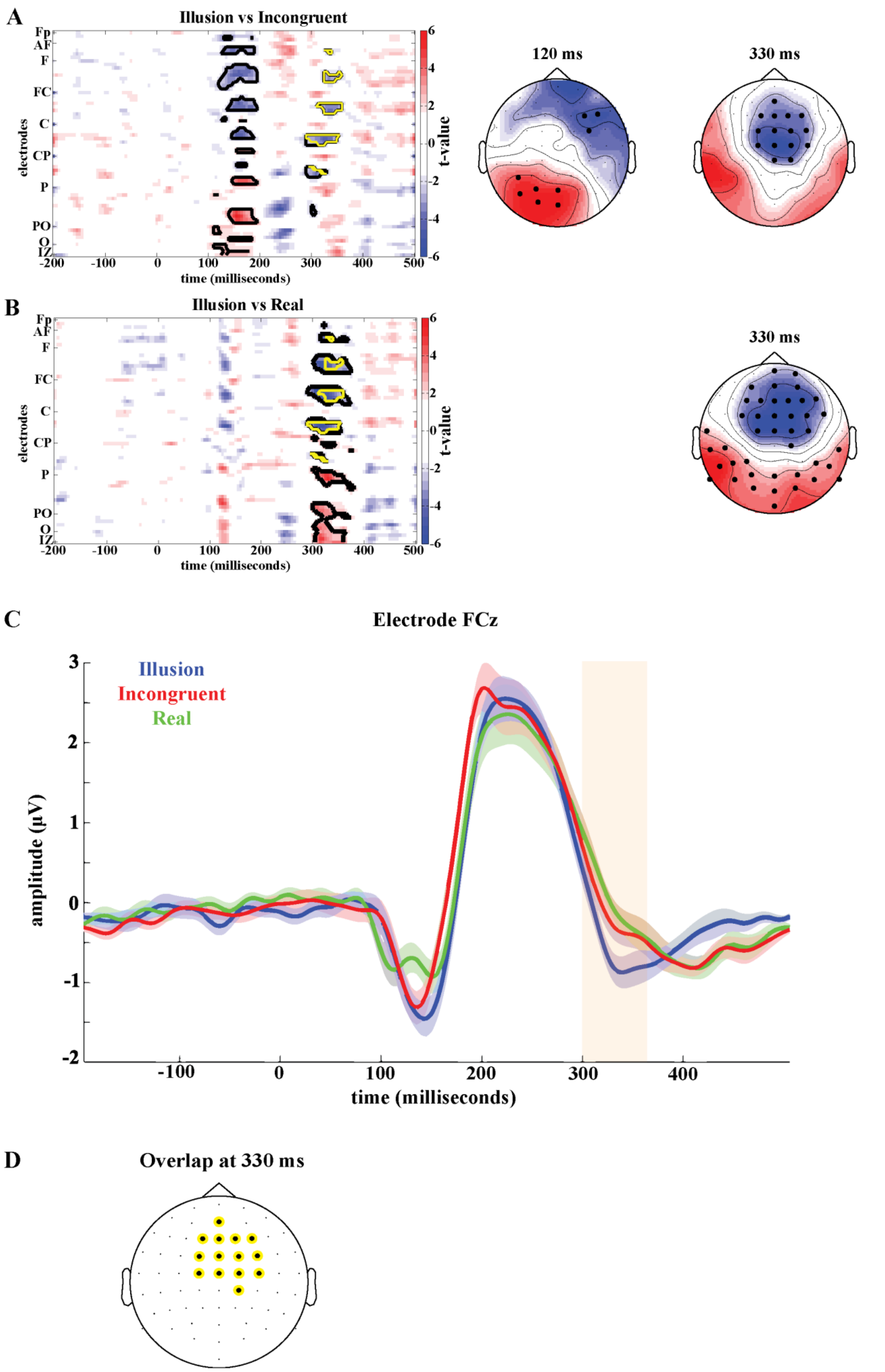


Figure 8| Illusion effect. (A) T-maps of the Illusion vs. Incongruent contrast (top) and the Illusion vs. Real contrast (bottom). Significant clusters (permutation statistics, $p < 0.05$, n=20) are highlighted in black, significant clusters common to

both contrasts are indicated in yellow. (B) Scalp topographies of t-values with significant clusters highlighted. (C) Grand-averaged event-related potentials at FCz of Illusion (blue), Incongruent (red) and Real (green). The shaded areas indicate the standard errors of the mean. (D) Overlap of significant electrodes between Illusion vs. Incongruent contrast and Illusion vs. Real contrast at 330 ms post-stimulus.

Illusion effect – Oscillatory activity

The illusion contrasts applied to the power of oscillatory activity revealed significant clusters of 19 electrodes in parietal areas where alpha power (8-12Hz) was lower in the Illusion compared to the Incongruent condition (Tsum = -77.4, $p<0.05$; Figure 9A, top left topography), and lower in the Illusion compared to the Real condition (Tsum = -80.4, $p<0.05$, Figure 9A, bottom left topography). In the beta band (13-25Hz) a cluster of 38 electrodes over frontoparietal regions also showed reduced power during the Illusion condition compared to the Incongruent (Tsum = -109.1, $p<0.05$, Figure 9A, top right topography) and Real conditions (Tsum = -178.2, $p<0.05$, Figure 9A, bottom right topography). The overlap of significant illusion effects for each band is shown in Figure 9B.

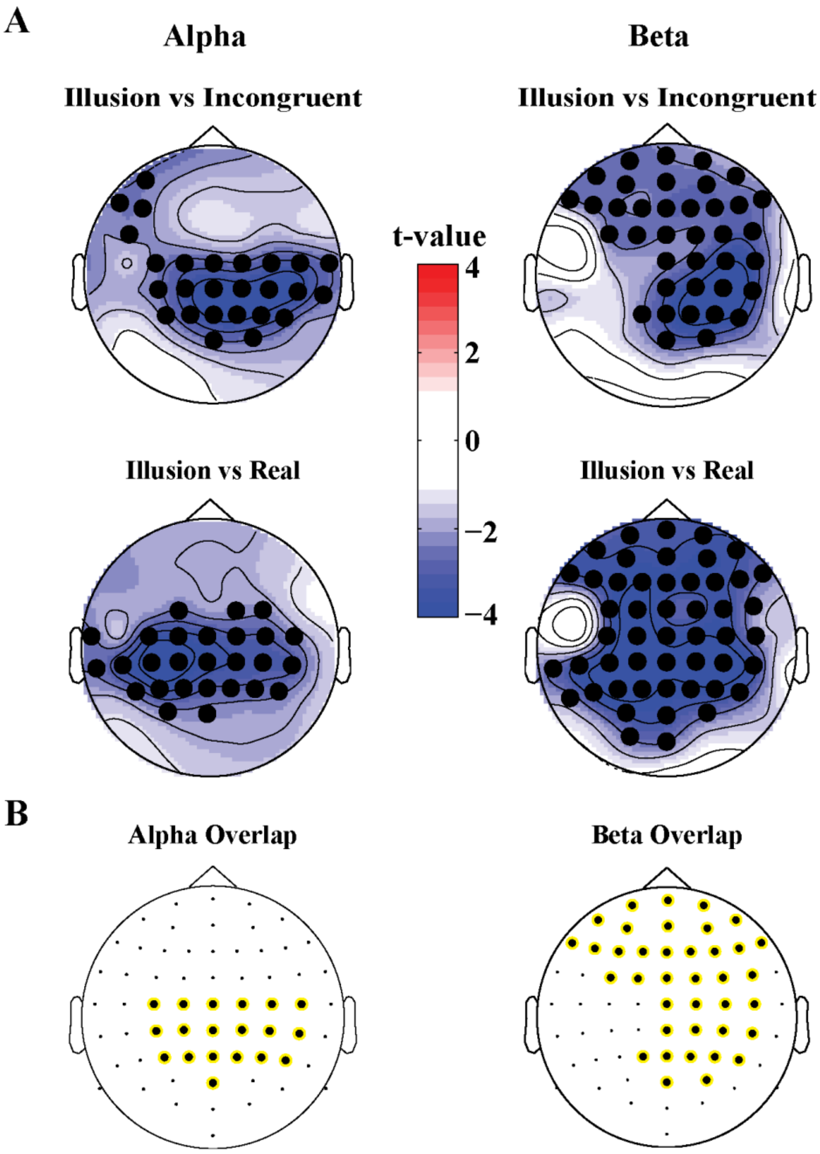


Figure 9| (A) Scalp topographies of t-values for differences in alpha (8-12 Hz, left panel) and beta power (13-25 Hz, right panel) for the Illusion vs. Incongruent (top panel) and Illusion vs. Real (bottom panel) contrast. Significant clusters (permutation statistics; $p < .05$, n=20) are highlighted in black. (B) Overlap of significant clusters between the Illusion vs. Incongruent and Illusion vs. Real contrasts.

Attention and Body-stimulus position contrasts

Potential confounding effects of changes in spatial attention and body-stimulus position were quantified using four additional experimental conditions analysed in a 2x2 design (Figure 7B). No significant effects were found when analysing the interaction between the factors Attention and Body-stimulus position. However, significant effects emerged in the attention contrast around 100 ms (Positive cluster: Tsum = 701.0, $p<0.05$; Negative cluster: Tsum = 728.0, $p<0.05$) and 250 ms (Positive cluster: Tsum = 687.7, $p<0.05$; Negative cluster: Tsum = -470.4, $p<0.05$; Figure 10A) in frontal and parietal regions. Significant effects in the body-stimulus position contrast emerged around 180 ms centred around electrode FCz (Tsum = -474.6, $p<0.05$; Figure 10B).

While the timing and location of the attention effects do not resemble the illusion effect, the topography of significant effects in the body-stimulus position contrast closely resembles the topography of the illusion effect (c.f. Figure 8D). The electrodes consistently involved in both effects comprised medial central and centrofrontal electrodes (Figure 10C), making it possible that potentially similar regions are involved in mediating the illusion and body-stimulus effects, but reflect these at distinct latencies relative to the stimulus.

We found no significant differences in oscillatory responses in the attention and body-stimulus position contrasts in either the alpha (8-12Hz) or beta band (13-25 Hz).

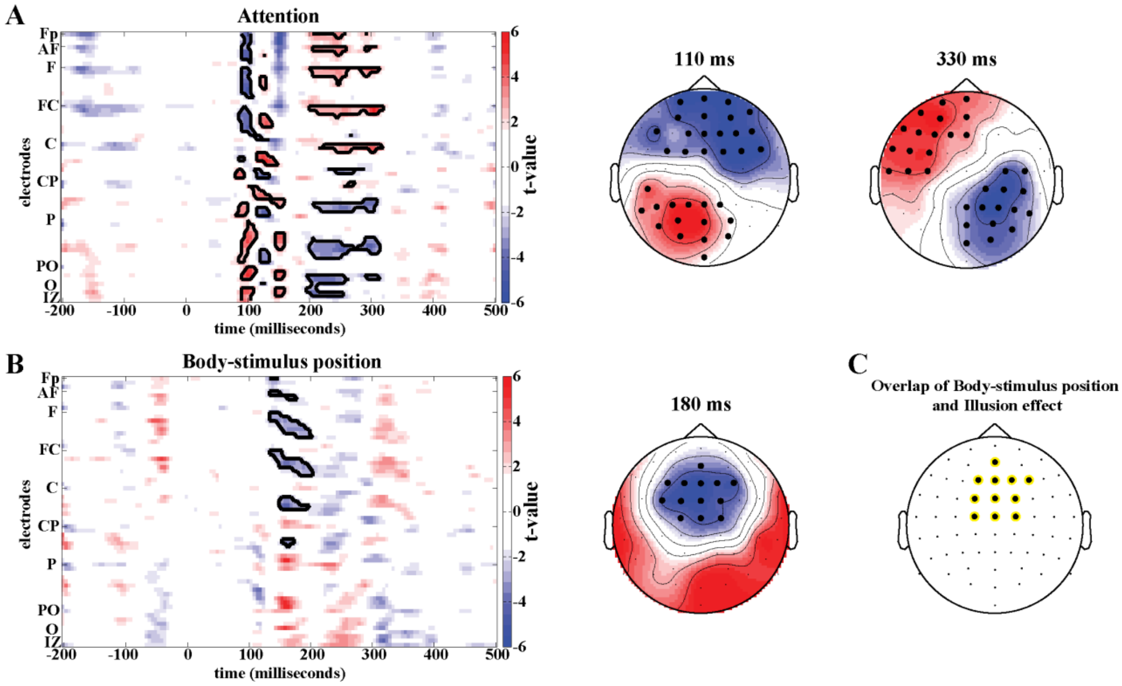


Figure 10| Contrasts for the effects of Attention and Body-stimulus position. (A) T-maps for Attention (top) and Body-stimulus position contrasts (bottom). Significant clusters (permutation statistics; $p < 0.05$, n=20) are highlighted in black. (B) Scalp topographies of t-values with significant clusters highlighted. (C) Overlap of significant clusters between the illusion effect (from Figure 8D) and the body-stimulus position effect.

Experiment 3

Behavioural data

Illusion onset occurred on average 46.7 ± 32.7 seconds (mean ± SD) after the start of stimulation onset in the illusion blocks. Five participants lost the feeling of the illusion after its initial onset. This occurred either in all three of the blocks (Participant 1, 2) or a single block (Participant 3, 4, 5). The resulting non-illusion sequences lasted on average 30.2 ± 27.1 seconds (mean ± SD). No illusion sequences were reported in any Incongruent blocks.

Illusion effect – ERPs

In the second experiment we compared the Illusion to the Incongruent condition while manipulating the duration of the visuo-tactile stimulation. We then performed a repeated-measures ANOVA on the ERP amplitudes at the time-electrode cluster identified by the illusion effect in experiment 2 (c.f. Figure 8D) to test the effects of illusion and stimulus duration (Table 1 & Figure 11). This confirmed a main effect of illusion at 330ms in this second dataset ($F_{(1,19)}=16.08$, $p<0.05$, $\eta^2p=0.46$), and revealed an effect of stimulus duration ($F_{(1.63,31.02)}=21.318$, $p<0.05$, $\eta^2p=0.53$) but no significant interaction ($F_{(2.81,53.40)}=0.235$, $p=0.860$, $\eta^2p=0.012$).

Condition	**Stimulus duration**			
	100 ms	**125 ms**	**150 ms**	**175 ms**
Illusion	-0.6652 (0.8934)	-0.3829 (0.6558)	-0.0917 (0.5668)	0.0138 (0.4904)
Incongruent	-0.4447 (0.7040)	-0.1790 (0.7211)	0.2105 (0.6217)	0.2503 (0.6161)

Table 1| Group means and standard deviations of amplitudes (μV) at 330ms post-stimulus in experiment 3.

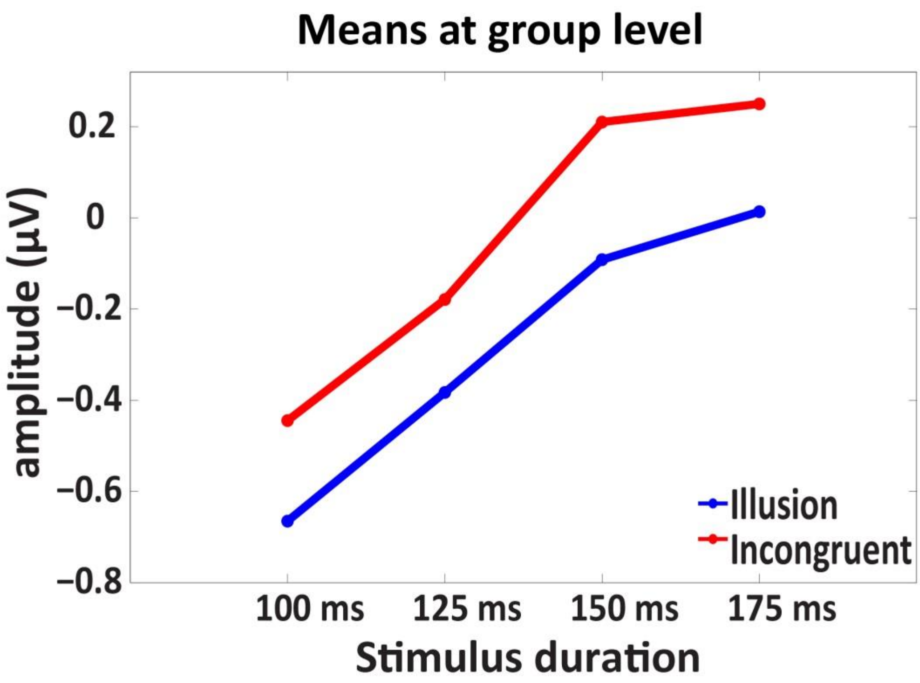


Figure 11|Group means of ERP amplitudes (µV) at 330ms post-stimulus in experiment 3.

Illusion effect – Oscillatory activity

For alpha power we found a main effect of illusion ($F_{(1.00,19.00)}$=16.407, p<0.05, η^2p =0.46) but no effect of stimulus duration ($F_{(2.69,51.08)}$=2.822, p=0.053, η^2p =0.13) and no significant interaction ($F_{(2.36,44.85)}$=2.860, p=0.059, η^2p =0.13). For beta power we found a main effect of illusion ($F_{(1.00,19.00)}$=15.337, p<0.05, η^2p =0.45) but no main effect of stimulus duration ($F_{(2.36,44.84)}$=2.917, p=0.056, η^2p =0.13). However, a significant interaction between illusion presence and stimulus duration was present ($F_{(2.28,43.33)}$= 7.533, p<0.05, η^2p =0.28). This interaction appeared to be driven by higher beta power for the stimulus duration of 100ms compared to the other durations in the illusion condition (Table 2 & Figure 12).

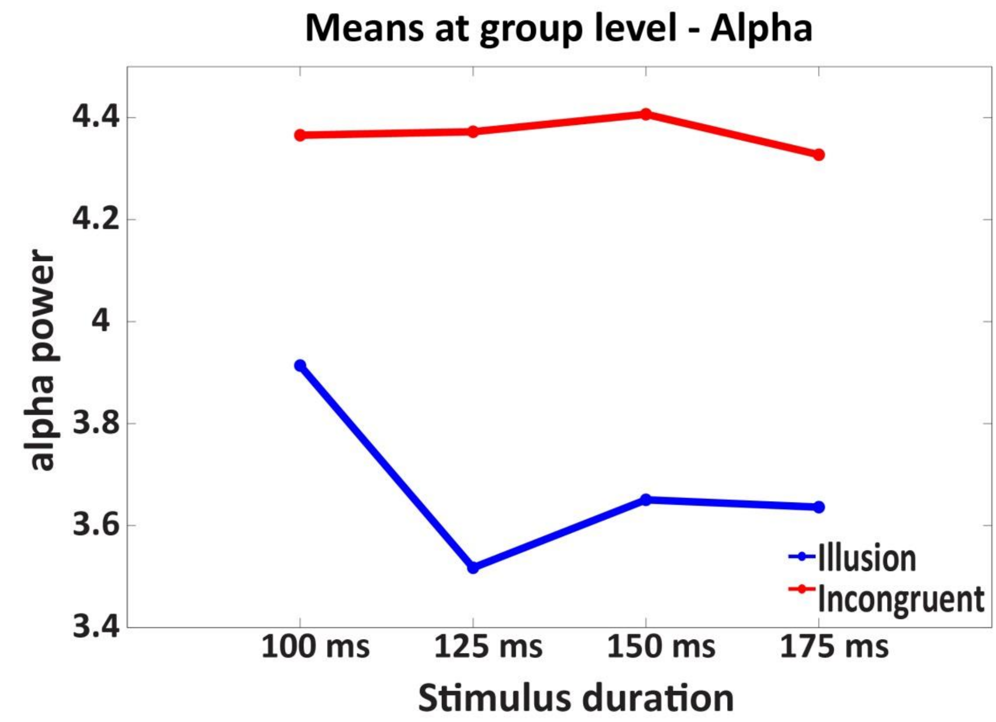
Alpha (8-12 Hz)

Condition	Stimulus duration			
	100 ms	**125 ms**	**150 ms**	**175 ms**
Illusion	3.9137 (1.9996)	3.5172 (1.7485)	3.6505 (1.7688)	3.6360 (2.0241)
Incongruent	4.3655 (2.1172)	4.3723 (2.0797)	4.4066 (2.1775)	4.3273 (2.0935)

Beta (13-25 Hz)

Condition	Stimulus duration			
	100 ms	**125 ms**	**150 ms**	**175 ms**
Illusion	1.0390 (0.4441)	0.9808 (0.4092)	0.9843 (0.4028)	0.9748 (0.4180)
Incongruent	1.0778 (0.4461)	1.1071 (0.4672)	1.0895 (0.4380)	1.0897 (0.4432)

Table 2| Mean values and standard deviations of oscillatory power in alpha (8-12 Hz) and beta band (13-25 Hz) in experiment 3.



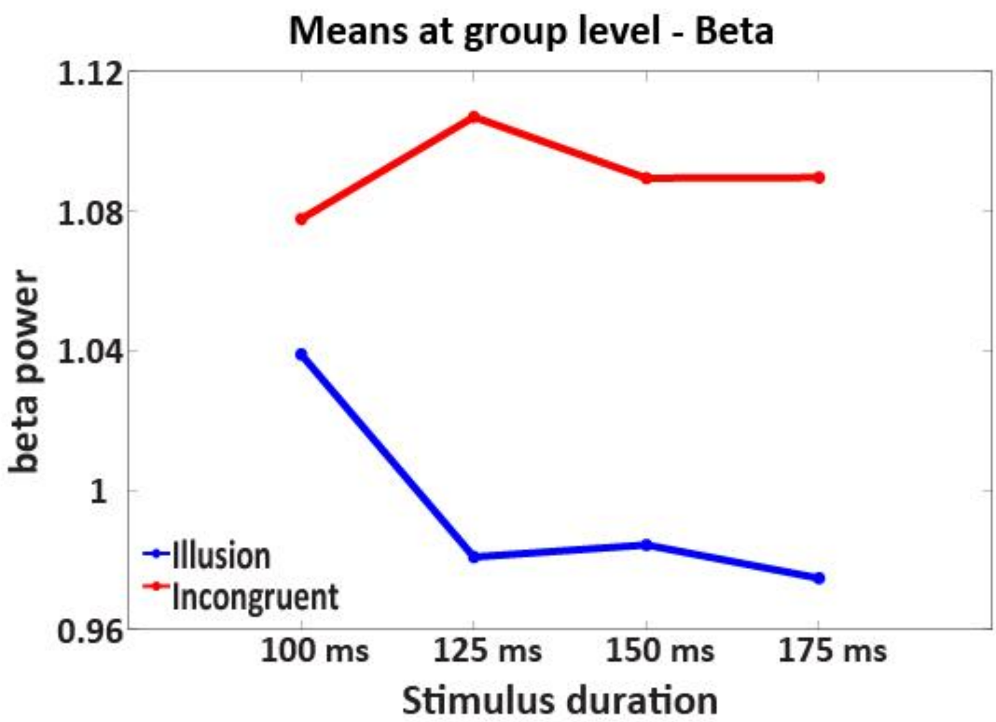


Figure 12| Group means of oscillatory power in alpha (8-12 Hz) and beta band (13-25 Hz) in experiment 3.

Discussion

We studied the neurophysiological correlates of the rubber hand illusion using a fully automated and precisely-timed visuo-tactile setup and a combination of experimental conditions. Across two studies and two control conditions we reliably found an illusion-related attenuation of ERPs around 330 ms over frontocentral electrodes. This effect was not related to attention or body-stimulus position confounds and was robust against changes in stimulus duration. We furthermore found that oscillatory activity in the alpha and beta bands was reliably reduced during the illusion. We thereby provide multiple neural markers of the RHI.

Illusion effects in evoked responses

Several previous EEG studies have aimed to understand the neural correlates and mechanisms underlying the illusory percept of body ownership in the RHI. These studies compared the evoked responses associated with the tactile stimulus on the participant's hand between conditions inducing the illusion and control conditions. The rationale behind this approach is to see whether and how the cortical representation of the tactile stimulus changes when its subjective location changes from the actual hand to the rubber hand. Previous studies differed regarding the latency of such an illusion-correlate in ERPs, reporting either early effects around 55 ms (Zeller et al., 2015) or much later effects around 460 ms (Peled et al., 2003). However, both studies relied on the manual stimulation by a brush handled by an experimenter, whereby each individual brush stroke can differ in timing and intensity. This variability in the sensory stimulus can be detrimental for measuring the timing and shape of the respective sensory evoked responses. To overcome this problem we here designed an automated setup that allows visuo-tactile stimulation with great temporal fidelity and consistency across trials. Furthermore, we asked subjects to indicate the onset of the rubber hand illusion during each trial and hence were able to include only those stimulation events in the analysis during which subjects actually reported the presence of the RHI. To facilitate this we only considered participants that had previously and reliably experienced ownership over a rubber hand and were familiar with the sensations associated with onset and presence of the RHI as determined by a pilot session.

To establish neural correlates of the RHI a comparison of the illusion condition with a control condition is required. Most previous ERP studies relied on the Incongruent condition in which the rubber hand is placed at an anatomically incongruent angle, or relied on the Real condition in which the rubber hand is absent and stimulation occurs on the real hand in view (Peled et al., 2003; Zeller et al., 2015, 2016). Using only one control condition makes the implicit and critical assumption that the illusion and control conditions differ only in a single factor, the presence of the subjective illusion. Yet, closer inspection of these conditions suggests that these may differ by other factors as well, such as focus of attention and body-stimulus position in the Incongruent condition, or the absence of a rubber hand in the Real condition. We therefore relied on the combination of control conditions to identify potential changes in evoked activity that are reliably associated with the illusion. The need to consider multiple control conditions is further demonstrated by the observation that some significant ERP effects were observed only in one of the two illusion vs control contrasts (c.f. Fig. 2). For example, the Illusion-Incongruent difference revealed a significant effect around 150 ms, which was absent in the Illusion-Real difference, and hence unlikely is a correlate of the subjective illusion. This suggests that results on the neural correlates of illusory body ownership that were obtained using a single control condition have to be considered with care.

We found neural activations that were reliably associated with the illusion only at longer latencies (here 330 ms) over frontocentral regions. Furthermore, this illusion effect did not interact with changes in stimulus duration. Together this suggests that these activations do not reflect processes related to early sensory encoding but rather reflect late and higher-order processes. Thereby our results differ from Zeller et al. (2015) who reported illusion related activity as early as 55 ms, but also differ from those of Peled et al. (2003), who found illusion related activity around 460ms. The discrepancies are possibly due to several factors: First, these previous studies relied on the manual stimulation by a brush, as opposed to the automated visual-tactile stimuli in the current study. Second, Zeller et al. restricted their analysis to activity before 300 ms post-stimulus, while Peled et al. only tested at specific time points not including 330 ms. This makes it difficult to compare significant effects across studies, as each relied on distinct time windows where potential effects were expected and contrasted using methods for multiple comparison . Third, the study by Zeller et al. relied on a rather small sample size (n=13), while we here relied on a sample size of n=20 participants in each experiment, which is considered to be the minimal sample size for neuroimaging studies based on concerns of reporting false positive results (Poldrack et al., 2017; Simmons et al., 2011). Fourth, the study of Zeller et al. reported significant illusion effects only for stimulation on the right hand, while we here focused on the subject's left hand, as previous studies have suggested a strong link between the right hemisphere and awareness of the subjective experience of body ownership (Frassinetti et al., 2008; Karnath and Baier, 2010; Tsakiris et al., 2007). Last but not least, we replicated the illusion effect around 330 ms in two independent studies, providing further evidence for the robustness of our result.

Neural origins of illusion-related activations

While the exact local neurophysiological sources of the illusion effect in the current study cannot be identified, its frontocentral location provides support for a pivotal role of premotor and possibly intraparietal areas in illusory hand ownership. Several studies have consistently associated activity in the ventral premotor and/or posterior parietal cortex with the illusory percept of ownership and hand position in the RHI (Brozzoli et al., 2012; Guterstam et al., 2015; Kanayama et al., 2016; Limanowski and Blankenburg, 2015; Petkova et al., 2011). Furthermore, Limanowski et al. (2015) and Guterstam et al. (2015) reported increased functional coupling between intra-parietal regions and premotor cortices during the illusion compared to control conditions. Both regions are ideal candidates for mediating the multisensory integrative processes that underlie the RHI. They process signals involved in self-attribution of the hand (Ehrsson, 2004; Evans and Blanke, 2013; Tsakiris et al., 2007) and analogous regions in the monkey brain have been found to contain trimodal neurons that integrate tactile, visual and proprioceptive signals (Fogassi et al., 1996; Graziano et al., 1997; Graziano and Gandhi, 2000; Iriki et al., 1996). Based on the topography of illusion-related ERP effects our data further corroborate a central role of motor-related regions in the body illusion.

This interpretation is further supported by the timing of the illusion effect, which matches results from intracranial recording studies, which have reported correlates of multisensory integration between 280 and 330 ms over precentral and postcentral regions adjacent to premotor cortex and IPS (Quinn et al., 2014). Similar late latencies were also reported for the integration of visual and somatosensory stimuli in parietal association cortex (Lippert et al., 2013). The attenuation of the evoked potential at 330ms during the illusion condition observed here could thus be indicative of the integration of visual, tactile, and proprioceptive information within the parietal-premotor network, which then results in the illusory percept of ownership and hand position in the RHI.

We did not administer any behavioural or physiological measures to measure the RHI, such as proprioceptive drift measurements or changes in body temperature. The reason for this was twofold. Firstly, we relied on a subjective measure of the illusion, as it allowed for uninterrupted recording of EEG data across all conditions. Secondly, our study aimed to identify the correlates of the ownership aspect of the RHI. As shown recently, proprioceptive drift does not provide a reliable assessment of this ownership aspect (Asai, 2015; Rohde et al., 2011). Rather, subjective ownership and the proprioceptive drift can be dissociated, with the latter measuring the spatial updating of the body in space rather than the strength of ownership over the rubber hand itself.

Illusion, attention and body-stimulus position

We used additional control conditions to reliably dissociate the neural correlates of the RHI from attention and body-stimulus position related activity. Specifically, we identified the timing and location of attention / body-stimulus position related effects and compared these to the activations revealed by the two statistical contrasts obtained from the Illusion. By comparing conditions where the visual stimulus was near the body with conditions where the visual stimulus was far from the body, we found body-stimulus position related processing to be associated with activity in frontocentral areas around 180 ms. This is in line with previous studies investigating the influence of proximity of hands and visual stimuli. For example, Reed et al. (2013) recorded ERPs during a visual detection task in which the hand was placed near or kept far from the stimuli. Similar to the results of the current study, they found increased negativity in the Nd1 component around 180 ms in the near hand condition (see also Sambo and Forster, 2009). The timing of the body-stimulus position related activity (~180 ms) was notably different from that of the illusion effect (~330 ms). This differentiates the illusion effect from body-stimulus position related activity. However, the topography of the body-stimulus position related activity at 180 ms was highly similar to that of our illusion effect at 330 ms. Thus, it is possible that both effects may emanate from the same cortical networks related to body processing. Support for this comes from a study by Brozzoli et al. (2012) who measured BOLD response while presenting participants with visual stimuli occurring next or distant from their hands. Their results indicated increased activity in premotor and intraparietal cortices in the condition where the stimulus was close to the hand compared to the condition where the stimulus was distant form the hand. Similar results were obtained when the participant's hand was replaced by a rubber hand on which the RHI was induced (Brozzoli et al., 2012). This suggests that both, the effects of body-stimulus position and the illusion may originate from processing in the intraparietal-premotor network but do so at different latencies relative to stimulus onset, further corroborating that the ERP correlates of the illusory percept reflect sensory integration processes in the parietal-premotor network.

We found attention related activity in frontal and parietal regions around 100 ms and around 250 ms. This timing is in agreement with previous ERP studies on visual-tactile attention which presented simultaneous stimuli in close proximity or at distant locations (Eimer and Driver, 2001; Sambo and Forster, 2009) and reported modulations of amplitudes between 80-125 ms and 200-280 ms associated with the induced changes in spatial attention. Interestingly the timing and location of activity related to attentional processing in our study is similar to the timing and location of early differences between Illusion and Incongruent. This could mean that these early differences in evoked potentials between Illusion and Incongruent condition are not directly related to the illusion but rather reflect the difference in attention focus between the two conditions. This underlines that the Incongruent condition, one of the most commonly used control condition in EEG experiments on the RHI, should be used with caution when trying to determine the neurophysiological correlates of the RHI.

Illusion effects in oscillatory activity

The analysis of oscillatory activity revealed that illusory hand ownership resulted in a relative decrease of oscillatory power in the alpha and beta bands. Modulations of alpha power have previously been implicated in the rubber hand illusion (Evans and Blanke, 2013) as well as the full body illusion (Lenggenhager et al., 2011). Our results are also in good agreement with those from a recent study on the somatic RHI (Faivre et al., 2017), a variant of the conventional RHI. Very similar to our results this study found a relative decrease in alpha power over frontocentral regions contralateral to stimulation site and a relative decrease in beta power bilaterally over frontoparietal regions during the illusion. Combined with the consistency of these power decreases across two control conditions and two experiments as shown here, this implicates that the decrease in alpha and beta power during the illusion is not associated with visual information or a specific control condition. Instead, it is likely to be directly tied to the feeling of ownership during the illusion itself, and hence constitutes a robust physiological marker of body ownership.

Limitations

We developed a fully-automated, temporally precise stimulation apparatus for induction of the RHI in our study. This allowed for the recording of evoked activity time-locked to the administered visuo-tactile stimuli, but resulted in a less naturalistic stimulation compared to the conventional manual stimulation (Peled et al., 2003; Zeller et al., 2015). This unnaturalness was consistent across the Illusion and control conditions and thus is very unlikely to have introduced differences between conditions in the current results. Yet it could potentially account for differences between the current and previous results. Future studies could explore this possibility by e.g. using an automated stimulation apparatus with motor-driven rods/brushes, providing a more naturalistic stimulation in addition to temporal precision.

All participants in the study were familiar with the illusion as they had previously indicated the experience of this illusion and had completed the RHI Questionnaire (Botvinick and Cohen, 1998). We only tested previously screened participants to facilitate the analysis of brain activity in response to the illusion, as this necessary requires participants that reliably experience the illusion for a sufficiently long period of time.

While this selection of participants was necessary to test for statistical differences between the Illusion and control conditions, future research should examine the neurophysiological processes that differ between subjects who experience the illusion and subjects who do not, or could test how illusion-related brain activity builds up in response to experiencing the illusion the first time, or over multiple times of exposure.

Finally, and this pertains all research on the neurophysiological correlates of illusory hand ownership, it is important to keep in mind that the illusion condition might differ from any control condition in factors not easily measured, such as a participant's increased state of introspection or arousal. This illustrates the importance of improving the quality of control conditions in further research on the subjective experience of the RHI.

Conclusion

We identified neurophysiological correlates of the rubber hand illusion in a reduction of alpha and beta power as well as in an attenuation of evoked responses around 330 ms over central electrodes. The attenuation of evoked responses is likely to reflect the integration of visual, somatosensory and proprioceptive information during the illusion, which then leads to the experience of ownership over the rubber hand. Our results furthermore emphasize the need to consider multiple control conditions in studies on body illusions, to avoid misidentifying effects related to changes in body-stimulus position or attention for correlates of illusory body ownership.

Chapter 5: Neurophysiological Correlates of the Somatic Rubber Hand Illusion in late Evoked and Alpha/Beta band Activity

Introduction

In the two experiments described in Chapter Four we suggested that the feeling of ownership in the RHI is associated with a reduction of alpha and beta power and an attenuation of evoked responses around 330ms over central electrodes. We concluded that these effects were likely to stem from activity in premotor and intraparietal areas which have previously been implicated in the illusory percept of hand ownership and hand position in the RHI (Brozzoli et al., 2012; Guterstam et al., 2015; Kanayama et al., 2016; Limanowski and Blankenburg, 2015; Petkova et al., 2011). However, when considering the visual processing that takes place during the RHI, there is another possible source for these effects. Evidence suggest that cells in the premotor cortex code visual inputs in a body-centred frame of reference (Graziano et al., 1994, 1997) in that they respond both when an object is seen approaching a specific body area and when this area is touched (Fogassi et al., 1992; Gentilucci et al., 1983; Graziano et al., 1994; Rizzolatti et al., 1981a, 1981b). As pointed out by Botvinick (2004) these cells are likely to be active after onset of the RHI when the hand-centred visual receptive fields become aligned with the rubber hand. The resulting premotor activity would then be related to the touch stimulus occurring on the remapped rubber hand rather than the actual processes underlying the feeling of ownership. In the current chapter our goal was to test that the attenuation of evoked responses around 330ms and the reduction in alpha and beta power in the Illusion condition as found in Chapter Four were not related to a remapping of visual receptive fields but to the feeling of ownership in the RHI.

To induce an illusory feeling of hand ownership in the absence of visual input i.e. without a change in hand-centred visual receptive fields we made use of the so called somatic rubber hand illusion (Davies et al., 2013; Ehrsson et al.; Faivre et al., 2017; Hara et al., 2015; Kodaka et al., 2014; Petkova et al., 2012; Pozeg et al., 2014; White et al., 2015a). The somatic rubber hand illusion was developed from the so-called self-touch illusion which was first reported by Ramachandran and Hirstein (1998). In their study an assistant was seated in front of a blindfolded participant whose index finger was guided to stroke and tap the assistant's nose by an experimenter. At the same time, the experimenter stroked and tapped the participant's own nose in synchrony. This synchronous tactile stimulation resulted not only in the participant feeling as if he/she was touching his/her own nose but also induced the sensation of the nose being dislocated or extended in space. This self-touch illusion was modified and adapted for illusory hand ownership by Ehrsson et al. (2005). To induce a somatic rubber hand illusion the participant's finger were guided to touch a rubber hand, while the participant's real hand was being touched by an experimenter in synchrony. Participants were instructed to press a foot pedal as soon as they started the illusion that the hand they were touching was their own. The study recorded fMRI data in this illusion condition and two control conditions- an asynchronous condition in which the touches occurred randomly and an incongruent condition in which the participant's finger was guided to touch a non-hand shaped object instead of the rubber hand. The results showed that despite the absence of visual input the somatic RHI was associated with greater bilateral activity in premotor regions compared to both control condition. This finding was in agreement with previous fMRI findings on increased premotor activity in the classical RHI (Ehrsson, 2004) prompting the authors to conclude that premotor activity in the classical RHI is unlikely to be associated with activity in remapped hand-centred visual receptive fields as suggested by Botvinick (2004). Applying a similar logic as Ehrsson et al. (2005), the current experiment compared ERPs and oscillatory activity in the somatic Rubber hand Illusion to establish if the neural correlates of the somatic rubber hand illusion are similar to the neurophysiological correlates of the classic RHI as identified in the two experiments described in chapter 4.

Probing the neural correlates of the somatic RHI in EEG brain activity required two modifications of the commonly used setup to avoid possible confounds. Firstly, the somatic rubber hand illusion is generally induced manually by an experimenter who applies direct touch to the participant's hand and guides the participant's finger to touch the rubber hand synchronously. However, manual stimulation cannot provide consistent stimulation across trials and is therefore not suitable for experiments using EEG. In addition, the presence of an experimenter during illusion experiments has been suggested to introduce various confounds (Rohde et al., 2013b). To overcome these problems, we developed an automated setup for inducing the somatic rubber hand illusion. The setup involved a stepper motor which guided the participant's finger to touch the rubber hand and a second stepper motor which guided a finger-shaped object to touch the participant's real hand. This setup delivered consistent stimulation across trials for each participant and did not require the presence of an experimenter. Secondly, we had to apply a novel control condition in order to allow for the recording of ERPs to similar touch stimuli across Illusion and control conditions. Commonly used control conditions in the somatic RHI such as the Incongruent condition and Asynchronous condition as described by Ehrsson et al. (2004) are not suitable for comparing ERPs across conditions. This is because the touch stimuli in these control conditions vary either in timing or texture from the touch stimuli in the illusion condition. In the current experiment we introduced a novel control condition in which the illusion is unlikely to occur because of an increased distance between rubber hand and the participant's real hand. This allowed us to directly compared touch evoked ERPs across illusion and control conditions.

In summary, in the current experiment our goal was to induce an illusory feeling of hand ownership in the absence of visual input by using the somatic RHI. We hypothesised that the somatic rubber hand illusion would be associated with an attenuation around 330ms post-stimulus on central electrodes and a reduction in alpha and beta power, as found in Chapter 4 in the classic RHI. A similarity between the results in the current experiment and the results in Chapter 4 would indicate that the illusion effects found in Chapter 4 were not merely related to a remapping of visual receptive fields as a result of the RHI but to the neurophysiological processes in the RHI itself.

Materials and Methods

Participants

A total of 34 right-handed volunteers participated in this study. We first ran a pilot study on all 34 participants, which involved two stimulation blocks of 2 minutes identical to the Illusion condition and Control condition described below. After each stimulation block participants rated the statement 'I felt as if I was touching my left hand with my right index finger' (Ehrsson et al., 2004). All participants strongly disagreed with the statement after the control condition block, while 20 of the 34 participants agreed or strongly agreed to the statement after the Illusion trial. Only these 20 participants were included in the current experiment (n=20 participants including 10 female, mean age = 20.8, years, SD = 3.6). All participants gave written informed consent before participation in this study. All protocols conducted in this study were approved by the Ethics Committee of the College of Science and Engineering of the University of Glasgow.

Experimental conditions and Procedure

Participants sat in a completely dark room comfortable chair in front of a wooden platform with two stepper motors (NEMA-17, 42mm) attached to it. The participant's left hand rested on the wooden board below a fixed stepper motor (Figure 13). A finger-shaped cylindrical putty cone was attached to this stepper motor in such a way that the tip of the cone repeatedly touched the dorsal part of the proximal phalanx of the participant's index finger when the stepper motor moved up and down. The participant's right hand was placed under a second movable stepper motor which had a ring attached to it. The ring was fitted around the participant's index finger's distal interphalangeal joint and the rubber hand was placed below the tip of the participant's index finger. Subsequently, when the stepper motor was set in motion the participant's fingertip repeatedly touched the dorsal part of the proximal phalanx of the rubber hand's index finger. The stepper motors were controlled via Matlab and an Arduino prototyping platform. Tactile stimulation was synchronous so that the participant's index finger touched the rubber hand at the same time as the putty cone touched the participant's left hand. To reduce eye movements, participants sat with their gaze fixed on a dimly illuminated 1 cm sized cross attached to the wall at eyeline height in 80cm distance in front of them. Participants wore ear plugs to reduce the noise caused by the stepper motors.

Each participant completed one block of the Illusion condition and one block of the Control condition. Illusion condition: The rubber hand was placed in parallel to the participant's left hand at a distance of 15cm (distance between middle fingers). The stepper motor guiding the participant's right index finger was adjusted accordingly. Control condition: The rubber hand was positioned at a distance of 85 cm to the participant's hand (distance between middle fingers) and angled 45˚. Besides this the setup was similar to the setup and stimulation protocol described in the Illusion condition. The condition sequence was randomized for each participant. Each block included 350 stimulation events. The tactile stimuli (i.e. the participant's fingertip touching the rubber hand and the putty cone touching the participant's hand) occurred within a time window of 100 ms after the stepper motors were set in motion. The timing of the touches varied across participants depending on finger anatomy, hand thickness and muscle tension but were consistent for each individual participant. The ISI between onset of the motor movement varied randomly and evenly between 900 ms and 1300 ms. Each block lasted approximately 5.5 minutes. Similar to Ehrsson et al. (2005) participants indicated verbally when they felt the onset of the illusion and when they lost the feeling of the illusion.

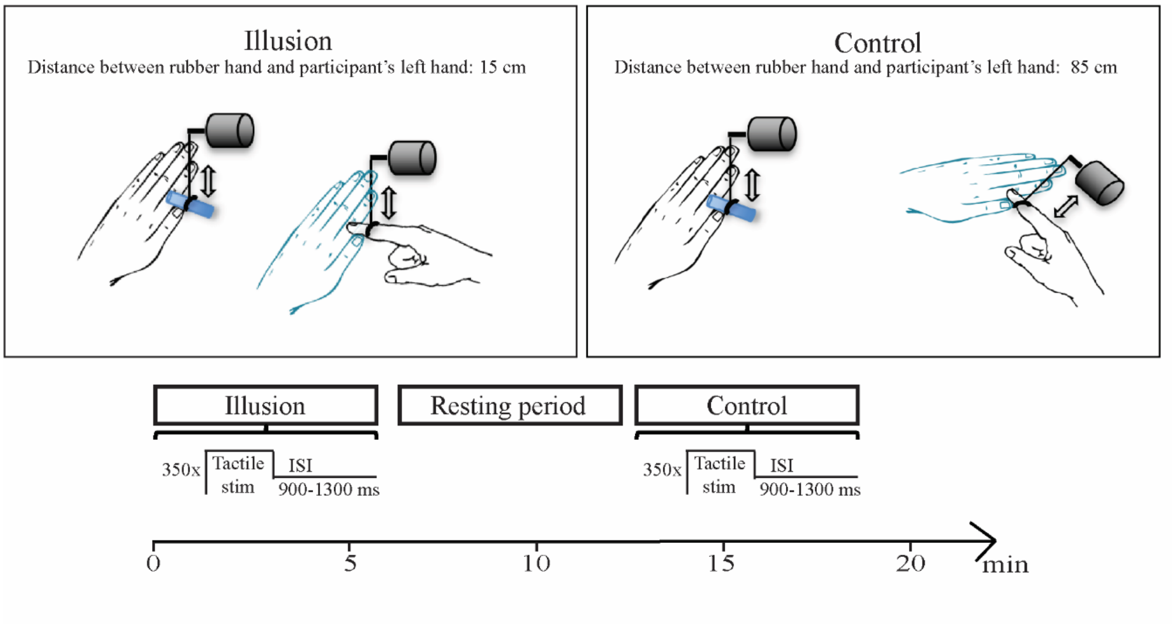


Figure 13|Stimulation and Experimental setup. Illusion condition: rubber hand placed in parallel to the participant's left hand at a distance of 15cm. Control condition: rubber hand was placed at a distance of 85 cm and angled 45°. The order of blocks was randomised for each participant.

EEG Recording

Experiments were performed in a darkened and electrically shielded room. EEG signals were continuously recorded using an active 64 channel BioSemi (BioSemi, B.V., The Netherlands) system with Ag-AgCl electrodes mounted on an elastic cap (BioSemi) according to the 10/20 system. Four additional electrodes were placed at the outer canthi and below the eyes to obtain the electro-occulogram (EOG). Electrode offsets were kept below 25 mV. Data were acquired at a sampling rate of 500 Hz using a low pass filter of 208 Hz.

EEG Analysis

Data analysis was carried out offline with MATLAB (The MathWorks Inc., Natick, MA) using the FieldTrip toolbox (Oostenveld et al., 2011). Stimulation events and their corresponding triggers were sorted based on condition and presence or absence of the illusion. For the analysis of the Illusion condition only events in which the illusion was present, as indicated by the subjects, were used. This amounted to 266±48 (mean±SD) events. For analysis of the control conditions only events in which the illusion was absent were used. Since no occurrence of the illusion was reported in the control condition, all respective events were included in the analysis. EEG data was segmented into epochs of 800 ms (200 ms pre-stimulus to 600 ms post-stimulus, stimulus defined as onset of the motor movement i.e. start of motor movement guiding the fingertip onto the rubber hand/ the putty cone onto the participant's left hand+100 ms) and pre-processed as described in chapter 4. According to the respective criteria we rejected of 34 ± 8 % of trials (mean ± SD). For further analysis the EEG signals were referenced to the mean EEG signal of near mastoid electrodes P9 and P10 to facilitate the recording of somatosensory related EEG activity. Condition averages of the evoked responses (ERPs) and oscillatory power were computed similar to the procedure described in experiment 2 and 3.

Our primary aims were to determine if ERP and oscillatory signatures of the somatic rubber hand illusion were similar to those of the classic rubber hand illusion as described in Chapter 4. Thus we compared average evoked responses at illusion effect electrodes and in a time window around the time point identified in Experiment 2. This time window was chosen as follows: Since in the illusion effect occurred 330 ms after stimulus onset in Experiment 2, the same was expected in the current experiment. However, in the current experiment the exact moment of stimulus onset, i.e. the moment the fingertip was touching the rubber hand and the putty cone was touching the participant's hands varied across participants. Taking into account the time the stepper motor took to move to its respective positions we estimated that the touch stimuli onset across participants varied within a time window of approximately 100 ms.

Subsequently, we choose to compare average evoked responses at illusion effect electrodes within a time window of 330 ms to 430 ms using a dependent t-test. Analysis of oscillatory activity was restricted to the respective illusion effect electrodes for alpha and beta band as identified in experiment 2. The average oscillatory power on these electrodes was compared using a dependent t-test. Both t-tests were computed one-tailed as both experiment 2 and 3 strongly suggested that an attenuation in both evoked responses and oscillatory responses was to be expected.

Results

Illusion onset occurred on average 84 ± 49 seconds after the start of stimulation onset in the illusion block. No participants lost the feeling of illusory hand ownership after its initial onset. No illusion sequences were reported in the control block. There was a significant difference in the average evoked response between the Illusion (0.43 ± 0.73) and the Control condition (0.67 ± 0.70) between 330 ms and 430 ms post-stimulus ($t(19) = -1.80$; $p < 0.05$, one-tailed) in that the Illusion condition showed an attenuation in the ERP. The grand-averaged evoked response in FCz is shown in Figure 14. We found no significant differences in oscillatory responses in the Illusion and Control condition in either the alpha band (8-12 Hz; $t(19) = 2.31$; $p = 0.98$, one-tailed) or beta band (13-25 Hz; $t(19) = 1.62$; $p = 0.94$, one-tailed; Table 3).

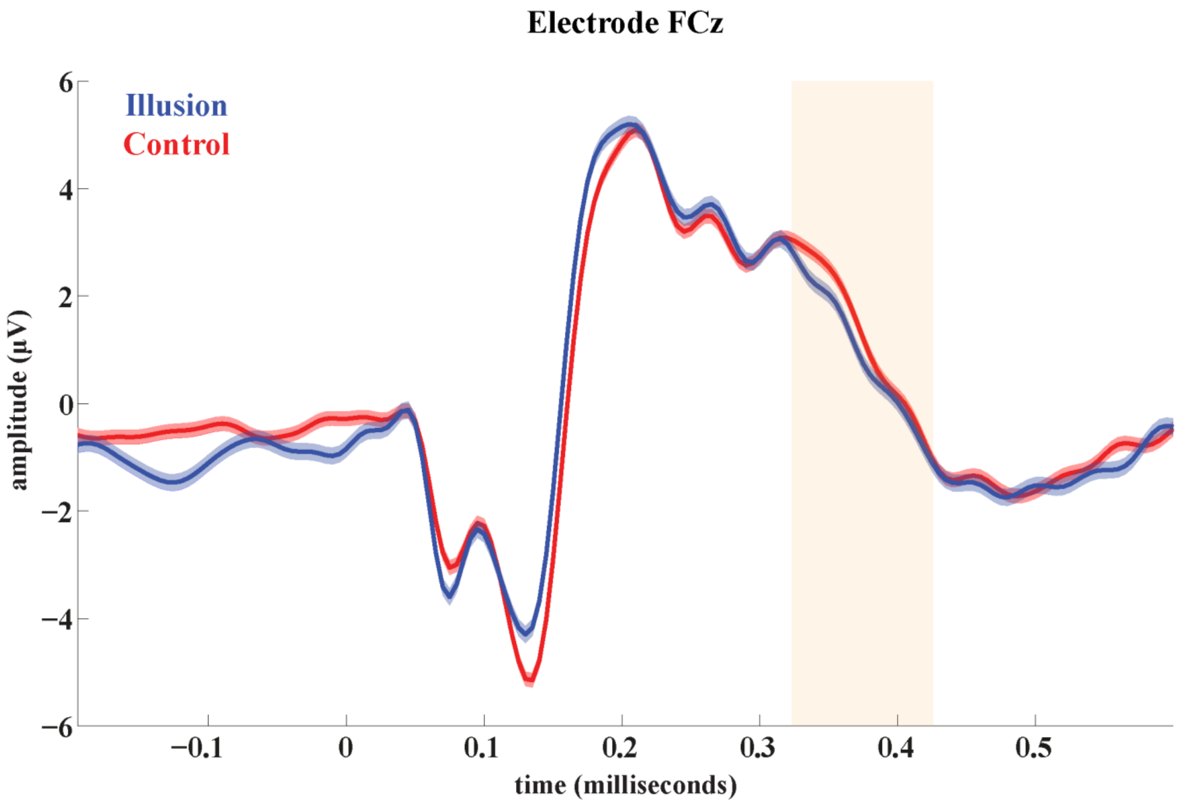


Figure 14|Grand-averaged event-related potentials at FCz in Illusion (blue) and Control (red) condition. The shaded areas indicate the standard error of the mean. The yellow shaded rectangle illustrates the analysed time window of 330ms-430 ms.

Condition	Alpha (8-12 Hz)	Beta (13-25 Hz)
Illusion	7.0127(5.6763)	1.4965(0.7850)
Incongruent	5.6966(3.8775)	1.3775(0.6119)

Table 3| Mean values and standard deviations of oscillatory power in alpha (8-12 Hz) and beta band (13-25 Hz)

Discussion

In the present study we studied the illusory feeling of hand ownership in the absence of visual input by using an automated setup to induce the somatic RHI. We found that the somatic rubber hand illusion was associated with an attenuation around 330ms post-stimulus on central electrodes similar to the RHI as described in Chapter 4. This provides evidence that the illusion effect in evoked responses as found in Chapter 4 does not merely reflect a remapping of visual receptive fields as a result of the RHI but the neurophysiological processes of the RHI itself.

Behavioural Results

In this experiment we introduced a novel fully automated setup for the somatic RHI which retained consistency of stimuli texture and quality across trials. It thereby allowed for the recording of somatosensory ERPs in the somatic RHI for the first time. Previous setups for inducing the somatic RHI relied on applying stimuli on the participant's hand by using either the experimenter's finger, automated vibration, or an automated tap by a robotic master-slave system. To compare our novel setup with previously used setups we recorded illusion onset times. We found that in our experiment illusion onset times were markedly longer than in previous experiments. Participants in our study reported the illusion onset after around 80 seconds, while previous studies noted illusion onset times of around 10- 15 seconds (Davies et al., 2013; Ehrsson et al.). The different onset times between studies are likely to be caused by the difference in stimuli quality and application. Both, Ehrsson et al. and Davies et al. relied on brushstrokes and touches applied and guided by an experimenter. The inconsistency in timing and quality across the applied stimuli may have led to a more rapid onset of a feeling of illusory hand ownership, similar to what has been found for the RHI (Rohde et al., 2011). In addition, the automated movement as induced by the stepper motor in our experiment was less naturalistic than movement induced by another person which might have added to the increase in illusion onset times. However, as can be seen in regard to the conventional RHI varying illusion onset times are not associated with a decrease in strength of illusory hand ownership (Ehrsson, 2004; Ide, 2013; Slater et al., 2009) . Thus, the delayed illusion onset time in the current setup presents no problem for the current experiment with its defined purpose. A second important parameter to compare our current setup's performance is how many participants successfully felt the somatic RHI. Previous studies on the somatic RHI reported that 25 out of 32 (Ehrsson et al., 2005) and 8 out of 12 (Petkova et al., 2012) participants felt the illusion. We found that in our experiment 20 out of 34 participants felt the illusion. With this ratio being similar to the previously reported ones we can conclude that despite a delayed illusion onset our novel fully automated setup can successfully induce illusory hand ownership in the somatic rubber hand illusion.

Neurophysiological results

Evoked responses

In chapter 4 we identified the neurophysiological correlates of the RHI in an attenuation of evoked response around 330ms over central electrodes. Considering the findings of previous fMRI studies on the RHI, we suggested that this attenuation provided further evidence for the involvement of premotor areas in illusory hand ownership. As noted by Botvinick (2004) however, there was a possibility that this premotor activity stemmed from a remapping of visual fields during the RHI rather than from processes directly related to illusory hand ownership. To investigate this possibility we used time point and location of the illusion effect identified in chapter 4 and tested if the average amplitude at this time point and location showed a significant attenuation in evoked responses associated with illusory hand ownership in a non-visual variant of the RHI, the somatic RHI. We found that similar to the conventional RHI, the somatic RHI shows an illusion-related attenuation around 330 ms on central electrodes. This suggests that this attenuation stems from brain activity both present in the conventional RHI and the somatic RHI. Since there was no informative visual information available in our experimental setup it is unlikely that this attenuation at 330 ms on central electrodes is then related to a remapping of visual fields as was suggested by Botvinick (2004). Rather, our findings suggest that this attenuation in evoked responses is associated with processes common in both illusions and directly related to illusory hand ownership. The current results should be considered with caution however because our setup did not allow us to determine the exact timing of the delivered touches. Further research is needed to create a setup that allows not only for consistency in stimuli texture but also for a precise measurement of when the touch stimuli occur.

Oscillatory activity

In chapter 4 analysis of oscillatory activity in the conventional RHI revealed that illusory hand ownership was associated with a reduction in alpha and beta power. In the current experiment on the somatic RHI, we found that illusory hand ownership did not result in a significant reduction of alpha and beta power, rather both alpha and beta showed an increase in power during the Illusion condition. There are two possible explanations for this. Firstly, a reduction in alpha and beta power might be directly related to a process that only occurs in the conventional RHI and not in the somatic Rubber hand illusion. As the lack of informative visual information is the main difference between the two illusions, it could therefore be suggested that the changes in oscillatory activity identified in chapter four are due to visual processing occurring in the conventional RHI. Since no visual processing of this kind occurs in the somatic RHI there would also not be a reduction in alpha and beta power. However, in a recent study Faivre et al. (2016) found evidence for a reduction in alpha and beta power in the somatic RHI. The failure to replicate these findings in our study might be due to the choice of our control condition. As Faivre et al. did not investigate evoked responses, they compared the illusion condition with a commonly used control condition in which the touches occurred asynchronously (Ehrsson et al.; Naish et al., 2012; Petkova et al., 2012; Pozeg et al., 2014; White et al., 2015b). As this control condition would have rendered the analysis of somatosensory evoked responses impossible we relied on a control condition in which we increased the distance and changed the angle between the participant's left hand and the rubber hand. This control condition might have involved processing associated with an increase in alpha and beta power. As a result it would have been more difficult to detect potentially subtle effects in oscillatory activity such as the attenuation in alpha and beta band that we identified in experiment two and three. In addition, our control condition might have been flawed in its ability to diminish the feeling of illusory hand ownership. While none of our participants reported feeling the illusion during this condition, Davies et al. (2013) found that illusory hand ownership in the somatic RHI was diminished though never abolished by distance and alignment manipulation in a synchronous condition. While Davies only tested distances of up to 60 cm which falls short of the 85 cm used in the current study, these results suggest that our control condition is not as consistent in abolishing the somatic RHI as e.g. the asynchronous condition used by Faivre et al. (2017). But why did participants in our study not report an onset of the illusion during the control condition? This might be due to the difference in intensity between the feeling of illusory hand ownership in the Control condition and the Illusion condition. If the participant associated the stronger feeling of illusory hand ownership as it occurs during the Illusion condition with the presence of the illusion, the diminished feeling in the Control condition could then go unreported. On the neurophysiological level however the control condition would not serve as a good control anymore as it has ceased to constitute a baseline. This might have resulted in a lack of statistical power to detect the differences in oscillatory activity between the illusion and the control condition. This possibility highlights the need for more objective measures of illusion presence and for refined control conditions in research on the somatic RHI. In order to further investigate the neurophysiological processes underlying the somatic RHI future studies should develop a control condition which abolishes the feeling of illusory hand ownership but retains consistency of stimuli texture and quality across trials. This would allow for a better comparison of both ERPs and oscillatory activity between illusion and control conditions as it limits possible confounds that could be mistaken for illusion effects.

Conclusions

We induced an illusory feeling of hand ownership in the absence of visual input by using an automated somatic RHI setup. We found that the somatic rubber hand illusion was associated with an attenuation around 330ms post-stimulus on central electrodes, as found in Chapter 4 in the classic RHI. The similarity between the results in the current experiment and the results in Chapter 4 indicates that this illusion effects in evoked responses is not merely related to a remapping of visual receptive fields as a result of the RHI but to the neurophysiological processes of the RHI itself.

Chapter 6: General Discussion

The work in this thesis systematically investigated the neurophysiological correlates of illusory hand ownership by using an automated RHI setup with variable parameters and applying high-density neuroimaging (EEG). This approach made it possible to identify the neural correlates of hand ownership in two variants of the RHI in evoked potentials and oscillatory activity across four experiments. As a result, the work presented here steps beyond previous EEG studies on the RHI and provides insights into the temporal dynamics of body ownership in the brain.

The first experiment (presented in Chapter Three), focused on establishing that the purpose-built, automated setup induced the Rubber Hand Illusion reliably, as measured by proprioceptive drift measurements and questionnaire ratings. The evoked visual and tactile responses elicited by the setup were identified. Timing and intensity of illusory hand ownership was found to be comparable to the existing literature. Further, the experiment identified necessary adjustments for the RHI setup in order to avoid confounds induced by avoidable differences between conditions in the subsequent experiments.

In the second experiment (presented in Chapter Four), a setup adjusted according to the findings of the first experiment was used to record evoked potentials and oscillatory responses in participants who experienced the rubber hand illusion. A combination of experimental conditions was applied to rule out confounds of attention, body-stimulus position and stimulus duration. We relied on of two control conditions to reveal the neural correlates of illusory hand ownership. The experiment revealed a reduction of alpha and beta power as well as an attenuation of evoked responses around 330 ms over central electrodes associated with illusory hand ownership. Further, the results indicated that body-stimulus processing and illusion processing as measured by evoked potentials might emanate from the same cortical network.

The third experiment (presented in Chapter Four) tested if the findings of the second experiment in regard to illusion effects were robust against changes in stimulus duration. Indeed, the reduction in alpha and beta power and the attenuation of evoked responses at 330 ms were found to be robust against changes in the length of the applied visuo-tactile stimuli. Together with the results from experiment two, these findings provide the first EEG marker of illusion related activity in the RHI induced by an automated setup with varying stimulus length. As both non-automated setups and invariable stimuli length have complicated the interpretation of previous EEG research on the RHI, the current results provide the first systematically derived insight into the temporal dynamics of illusory hand ownership in the brain.

Experiment four (presented in Chapter Five) investigated if the neural correlates identified in the second and third experiment were indeed related to the feeling of illusory hand ownership in the RHI and not to a mere remapping of visual receptive fields. To test this, evoked potentials and oscillatory responses were recorded during the somatic rubber hand illusion, a non-visual variant of the RHI. The somatic rubber hand illusion was found to be associated with an attenuation around 330 ms post-stimulus on central electrodes, similar to the classic RHI in experiment two and three. This indicated that this illusion effect in evoked potentials was not merely related to a remapping of visual receptive fields as a result of the RHI but to the neurophysiological processes of the RHI itself. This study constituted the first investigation of evoked potentials in the somatic RHI using an automated setup and consolidated the interpretation of the attenuation around 330 ms in evoked potentials as pertaining to illusory hand ownership processes.

Neural and functional origins of the attenuation in evoked potentials and oscillatory activity

The results of these experiments suggest that illusory hand ownership was associated with an attenuation around 330ms on frontocentral electrodes (Experiment two, three and four) and an attenuation in alpha and beta power (Experiment two and three). The following paragraphs explore how these results fit in with the current literature on body ownership.

Neural origins of the attenuation in evoked potentials

As the work in this thesis relied on EEG as its neuroimaging tool, the exact neurophysiological sources of the identified illusion effect cannot be directly identified. However, there is a strong body of evidence that our identified illusion effect in evoked potentials is a result of illusion related multisensory processing in premotor and/or parietal areas. Firstly, numerous fMRI studies on the rubber hand illusion have identified illusory hand ownership to be associated with processing in premotor and parietal regions (Bekrater-Bodmann et al., 2014; Brozzoli et al., 2012; Ehrsson, 2004; Gentile et al., 2013; Grivaz et al., 2017; Guterstam et al., 2014; Limanowski and Blankenburg, 2015; Petkova et al., 2011). Further, the timing of the illusion effect matches results from previous multisensory integration studies which reported visual-tactile integration related processing over precentral and postcentral regions adjacent to premotor cortex and intraparietal sulcus between 280 ms and 330 ms.

Further evidence in particular for parietal areas as the source of our illusion effect in evoked potentials emerges when we compare our results to findings derived from an EEG investigation on the Aristotle illusion. A tactuo-proprioceptive illusion in which one object touching the contact area between two crossed fingers is perceived as two lateral objects, the Aristotle illusion is not an illusion modulating body ownership but is still comparable to the RHI in that it is a multisensory illusion involving somatosensation and proprioception. In line with our results, Bufalari et al. (2014) found modulations in late evoked potentials over frontocentral electrodes in the Aristotle illusion (Bufalari et al., 2014). Source localisation revealed the source of these modulations to be in inferior parietal regions. These findings indicate that illusion related (and, in the case of the RHI, potentially ownership related) activity in such multisensory illusions occur in parietal areas and can manifest itself as modulations over frontocentral electrodes.

Further support for our suggestions that the attenuation in evoked potentials originates from processing within the premotor-parietal network is provided by the overlap of electrodes showing illusion effect and body-stimulus effect in experiment two. We found that body-stimulus processing related to the position of the visual stimulus in relation to the body, i.e. if the visual stimulus occurred on the body or not on the body, was associated with an attenuation at 180ms on frontocentral electrodes. This attenuation is likely to originate from activity in the peripersonal space (PPS) system as previous research has shown that this system integrates multisensory cues around the body, depending on the position of these stimuli in the surrounding environment with respect to the body (Makin et al., 2008). This multisensory integration in PPS has been shown to involve a range of brain areas, such as superior parietal cortex (Gentile et al., 2013, 2011;

Makin et al., 2008; Schaefer et al., 2012; Sereno and Huang, 2006), temporo-parietal cortex (Brozzoli et al., 2012, Gentile et al., 2013, 2011) and the premotor cortex (Brozzoli et al., 2012; Gentile et al., 2013, 2011). Notably, a recent meta-study by Grivaz et al. (2017) confirmed that PPS and body ownership share common neural substrates in parietal in premotor areas. This is in agreement with our finding in experiment two that, while occurring at different time points, the body-stimulus effect and illusion effect occurred at similar electrodes, i.e. frontocentral channels. This similar location in how both PPS system and body ownership activity emerged at the electrode level is indicative of similar neural origins. In conjunction with findings of Grivaz et al. (2017), we therefore have more evidence that the attenuation in evoked potentials around 330ms reflects processing in parietal and premotor areas.

The final piece of evidence that our identified illusion effect in evoked potentials is a result of illusion related multisensory processing in premotor and/or parietal areas emerges when the findings of experiment four are interpreted in context with previous research on bodily illusions beyond the RHI. In experiment four we found the attenuation at 330 ms on frontocentral electrodes in a non-visual variant of the RHI, the so-called somatic rubber hand illusion or self-touch illusion. Thus, the illusion-related change in evoked responses was identifiable in two different bodily illusions, the classic RHI and the somatic RHI. This hints at the possibility that this illusion effect might be related to the general processing involved in illusory body ownership. Notably, previous research on various bodily illusions has repeatedly found processing related to body ownership to be associated with activity in premotor and parietal cortices. For example, Petkova et al. (2011) induced a full body illusion, in which people experienced an artificial body to be their own, and fMRI analysis revealed a coupling between the experience of full-body ownership and neural responses in bilateral ventral premotor and left intraparietal cortices. Further, Apps et al. (2015) investigated the so called enfacement illusion, in which participants experience the sensation of looking at themselves in the mirror when in fact looking at another person's face, and found that the strength of this illusory experience correlated with activity in intraparietal areas. Thus, there is converging evidence that that both premotor and parietal regions are involved in generating a feeling of body ownership and in general body-illusion related processing across various kinds of illusions. This is in agreement with our result that illusory hand ownership in both the classic RHI and the somatic rubber hand illusion was related to an attenuation at 330 ms on frontocentral electrodes. Hence, our identified illusion effect at 330 ms in evoked potentials is likely to reflect higher-order multisensory integration processes involved in the origin of not only illusory hand ownership but illusory body ownership in premotor and parietal regions.

Predictive coding and the functional neural underpinnings of the RHI

While the involvement of premotor and parietal regions in illusory body ownership has been established, it is less known in what way these regions communicate with each other and other regions during the RHI. While the neurocognitive models of body ownership in the RHI suggested by Tsakiris (2010) and Makin et al. (2008) have attempted to outline a possible step-by-step process of how illusory hand ownership originates, separating neurophysiological multisensory integration processes from neurophysiological processes directly related to the feeling of illusory hand ownership remains difficult. Studies on the functional processes in the RHI have however provided glimpses into how illusory hand ownership emerges and is maintained. Using effective connectivity analysis, Gentile et al. (2013) were the first to report increased functional coupling of the left IPS with the PMv and the LOC during congruent visuo-tactile stimulation in an RHI inspired paradigm. This functional coupling was identified during the RHI by Limanowski and Blankenburg (2015) in an fMRI study which relied on an automatic stimulation setup for inducing illusory hand ownership. This study also demonstrated an information exchange between hierarchically lower areas in lateral occipital areas (LOC) and somatosensory cortex and the hierarchically higher intraparietal sulcus, and between the intraparietal sulcus and the premotor cortex. Notably, connections from both the somatosensory cortex and the LOC to the intraparietal sulcus were significantly enhanced under the RHI, meaning that activity within the intraparietal sulcus was more strongly causally influenced by modulations of the bottom- up connections from the somatosensory cortex and the LOC. A similar dynamic was also observed by Zeller et al. (2016) who used dynamic causal modelling on EEG data in the RHI. The researchers found a significant increase of forward connectivity between occipital areas and the premotor cortex and a decrease in intrinsic connectivity within primary somatosensory cortex. These findings indicate that during the RHI information exchange between hierarchically lower sensory areas such as the somatosensory cortex and the occipital cortex and hierarchically higher integration areas such as the premotor cortex and parietal areas increases. This communication between lower and higher areas identified in both EEG and fMRI studies on the RHI has been suggested to reflect hierarchical information exchange according to the principles of predictive coding (Zeller et al., 2016).

The predictive coding theory posits that the brain constructs hierarchical generative models about the causes of the sensory input it receives. It then continually attempts to minimize its models' prediction errors on each hierarchical level. To achieve this, the brain derives sensory predictions from its models. These predictions then get tested against incoming sensory input (Friston, 2010; Limanowski and Blankenburg, 2013). If there is a match between the predicted and actual sensory input, the model in question is confirmed. If there is a mismatch, prediction error occurs and the model needs to be updated (Friston, 2010; Friston et al., 2013). Apps and Tsakiris (2014) suggested how predictive coding can account for the different stages of the RHI. Everyday experience makes people predict that a touch they feel on their hand is associated to a touch they see on their hand. Before synchronous stimulation, the sensory input to the visual system has created predictions in the visual system that the participant is seeing a rubber hand which has been assigned a low probability that this is the participant's own hand. During visuo-tactile stimulation the temporal congruence between the visual stimulus on the rubber hand and the somatosensory stimulus on the real hand evokes surprise both in the somatosensory system and the visual system. This surprise is explained away by the top-down influence from multimodal areas and perceptual learning processes in the unimodal areas i.e. the model is updated. As a result, the probability that the visually perceived rubber hand is part of the participant's body increases. At the same time, the probability that this object is part of the body updates the probability that touch on the rubber hand will result in a touch experience. Subsequently during the resulting illusory hand ownership touch on the rubber hand is no longer surprising, as the object is perceived visually as part of one's body. In other words, the proprioceptive information about where the participant's real hand is located is explained away to accommodate a new model which reconciles the incoming sensory input from visual and somatosensory areas with a predicted input- I am looking at my own hand therefore I can feel and see touch on it.

These suggestions of how illusory hand ownership in the RHI emerges as a result of predictive coding processes are consistent with the above mentioned findings on the functional correlates of illusory hand ownership in the RHI by Gentile et al. (2013), Limanowski and Blankenburg (2015) and Zeller et al. (2016). The enhancement in connectivity between lateral occipital areas and somatosensory areas with the parietal cortex and premotor cortex that was identified by Gentile et al. and Limanowski et al. is likely to represent the ascending of the prediction errors from visual and somatosensory areas to the hierarchically higher parietal and premotor cortex. Zeller et al. (2016) suggested that the increase in connectivity between lateral occipital areas and the parietal cortex in particular represents a process of affording greater precision to the visual input, which in turn attenuates the precision of somatosensory and proprioceptive inputs, leading to a recalibration of felt hand position and ultimately to illusory hand ownership.

Our identified illusion effect in evoked potentials at 330 ms cannot be unequivocally assigned to a particular stage in this predictive coding model of the RHI. We can however speculate as to which functional step it may represent. Zeller at al. (2015) interpreted their finding of an attenuation in evoked potentials over parietal areas at around 55 ms in the illusion condition as a result of the attenuation of proprioceptive and mechanoreceptive input. The authors argued that the early timing of this effect supports this suggestion as such an attenuation after illusion onset would be established before multimodal integration of sensory afferents in hierarchical higher levels which is thought to occur earliest after around 100 ms post-stimulus. Our illusion effect in evoked potentials at 330 ms is therefore unlikely to reflect this early attenuation of proprioceptive and mechanoreceptive input but might relate to the later occurring illusion specific processes, such as integration of visual, somatosensory and proprioceptive input or the disownership of the real hand. While this underlines our illusion effect as a valuable marker for illusory hand ownership, identification of the exact computational process underlying its emergence will require further investigation in the future.

Neural and functional origins of the attenuation in alpha and beta band activity

In oscillatory brain activity, illusory hand ownership was associated with a relative decrease of oscillatory power in the alpha and beta band in the work of this thesis. Across experiment two and three we found a decrease in oscillatory alpha power over parietal areas and a decrease in oscillatory beta power over frontoparietal regions. These findings are in agreement with a recent study by Kanayama et al. (2016) who applied causality analysis during the RHI and found a reduction in connectivity from frontal areas to parietal areas at 3-20 Hz at 200 ms poststimulus. This reduction in connectivity was negatively correlated with the ownership score on a RHI questionnaire. This suggests that activity in alpha and beta band is strongly involved in illusory hand ownership by facilitating communication between frontal and parietal areas. Kanayama et al. (2016) suggested that the reduced connectivity between frontal and parietal areas might unlock the mechanisms preserving body integrity thereby allowing the rubber hand to be perceived as part of the participant’s body. Thus, the identified reduction in alpha and beta band power in the work of this thesis might relate to this process, too. Notably this loosening of body integrity would occur in any kind of body illusion and therefore the involvement of alpha and beta should be found in studies on illusions other than the RHI. Indeed, in particular for alpha this is the case. Lenggenhager et al. (2011) for example found modulated alpha band oscillations in the illusion condition in an experiment on the full body illusion. Further, Serino et al. (2015) found a decrease in alpha power in the illusion condition of a study investigating a movement dependent VR variant of the enfacement illusion. An illusion during which synchronous visual and tactile inputs update the mental representation of a participant's own face to assimilate another person's face (Serino et al., 2015). Considering the predictive coding account of illusory body ownership, alpha and beta band activity might thus play a role in enabling the communication between brain areas involved in the RHI. In support of this, alpha band and beta band activity have been suggested to be involved in shaping the functional architecture of the working by determining both engagement and disengagement of different regions (Haegens et al., 2011). This has been found in particular for the somatosensory cortex in studies involving the body. For example, Brinkman et al. (2014) used MEG to investigate changes in oscillatory power while participants imagined grasping a cylinder oriented at different angles. The authors found that alpha-band oscillatory power increased in the sensorimotor cortex ipsilateral to the arm used for imagery, whereas beta-band power concurrently decreased in the contralateral sensorimotor cortex. Similarly, Buchholz et al. (2014) found that beta oscillations increased excitability in contralateral cortex in a saccade task. The authors suggested that oscillatory activity in the beta band gates information flow throughout the sensorimotor network. This indicates that the identified decrease in alpha and beta power in the data presented here is involved in the communication between somatosensory and potentially higher hierarchical areas in the RHI. Further research is needed however to identify the exact underlying computational processes.

Applicability and Impact of our findings

The identification of the neurophysiological correlates of illusory hand ownership in evoked potentials and oscillatory activity in this thesis presents an important step towards facilitating clinical and technological applications of the rubber hand illusion and of other bodily illusions. As both, the attenuation around 330 ms in evoked potentials and the decrease in alpha and beta band power appear to be part of the EEG fingerprint of the illusion, these markers could be utilised as a new physiological measure of the RHI. A new, reliable, and temporally precise physiological measure for the RHI and other bodily illusion would present a much needed step towards the standardisation among experiments investigating body ownership (Ramakonar et al., 2011). This standardisation is becoming more and more important as the RHI has proven useful in improving diagnostics and ideas for therapeutic intervention for a range of different pathologies. For example, numerous studies report a link between susceptibility to illusory hand ownership and schizophrenia (Peled et al., 2000, 2003), and schizotypical personality traits (Asai et al., 2011). Further, Schaefer et al. (2013) demonstrated that alien hand syndrome can be affected by the somatic RHI and suggests that further investigation of this influence could lead to the developments of treatments in the future. Induction of the RHI has also been found to improve the symptoms of somatoparaphrenia. In a study on two patients with somatoparaphrenia, Bolognini et al. (2014) investigated whether a RHI, modified for this specific purpose, could induce a remission of the delusional beliefs concerning the left hand. The intervention induced an immediate self-reattribution of the left hand, with one patient showing long-lasting remission. These promising results underline the usefulness of interventions involving bodily illusions in clinical settings and the need for a standardised measure of illusory body ownership.

Besides the possibility of using our identified illusion effects as a marker for when ownership has been induced, they might also help in the quest of finding a way to directly induce a feeling of ownership over a fake limb/body without applying visual-tactile stimulation. Future advances in technology and in our functional understanding of the brain may make it possible to directly facilitate illusory body ownership via brain stimulation. This stimulation would require detailed knowledge of the temporal aspect of the neurophysiological processes underlying bodily illusions, which our results have shed light upon. The facilitation of body ownership through brain stimulation would be applicable mainly in two areas – immersive virtual environment technology and the rehabilitation of people with amputated limbs. In virtual reality (VR) and augmented reality (AR), inducing ownership towards a digital avatar enhances the degree of immersion and the user's physical performance (Gonzalez-Franco and Peck, 2018). Instantly establishing a user's body ownership of his/her virtual avatar would greatly facilitate the applicability of technology using VR or AR. In addition, establishing a feeling of ownership over neuro-prosthetic devices is a key goal in rehabilitative therapies for limb amputees (Collins et al., 2017). While advances have been made in creating prosthetic limbs which provide sensory feedback (Akhtar et al., 2018; Hsiao et al., 2011) facilitating body ownership over these artificial limbs in a direct way via brain stimulation would support acceptance and intuition of use. In summary, inducing body ownership over artificial limbs/bodies is of importance in both clinical and technological settings and the findings of the work contained in this thesis might provide a conceptually important step towards facilitating this process.

Limitations

In experiments one, two and three we applied visuo-tactile stimulation with the help of vibration motors and LED lamps as opposed to the brushstrokes commonly used in RHI experiments. This less naturalistic setup gave us flexible control over the duration of the stimuli and enabled us to record evoked potentials time locked to the visuo-tactile stimuli. In light of the predictive coding account of the RHI which places importance on the participant's previous experience regarding visuo-tactile stimuli on and surrounding their body, it can be argued that this unnaturalness might have impacted on our result. Vibratory stimuli paired with flashes of light are not a naturalistic occurrence and thereby might have interacted differently with the sensory models held by the brain compared to a more naturalistic brush stroke. Our stimulation however was successful in inducing the illusion in time frames similar to other experiments using brushstrokes indicating that the general computational processes underlying the onset of the illusion were similar. However, if possible our illusion effects should be investigated using a more naturalistic but temporally accurate stimulation setup to confirm this conclusion.

Further, our experiments did not control for wandering attention during the illusion condition. In experiments one, two and three participants were simply instructed to keep their eyes focussed on the LED situated on/close to the rubber hand and in experiment four participants had to focus on a fixation cross. While stimulation in all experiments was continuous throughout each trial and participants had a task at hand i.e. indicating if they experienced a feeling of illusory hand ownership, we cannot be sure if this sustained participants' attention throughout the trials. Future studies could possibly include background tasks involving the stimulation setup itself to increase the likelihood of participants' attention remaining focussed on the stimulation.

Finally, all our results are based on a very particular sample - people who successfully experienced illusory hand ownership in the RHI. Similar to most other studies on the RHI we excluded participants who did not experience the illusion within the trial duration of each experiment. While this allowed us to identify the neurophysiological correlates of the RHI in a within-subjects design, future studies should compare evoked potentials and oscillatory activity during stimulation between people who feel and who don't feel the illusion. This may help to dissociate processes related to multisensory processing from processes related to the conscious experience of body ownership and will shed further light onto the functional significance of the illusion effects reported here.

Future experiments

There are several avenues for future studies on the neurophysiological correlates of the RHI and of illusory body ownership in general. Most studies including those presented in this thesis have focussed on comparing neuroimaging data obtained in an illusion condition with that obtained in one or more control conditions. This approach however does not elucidate the mechanisms of the initial onset of the illusion, which is potentially one of the most informative processes for understanding the RHI on the neurophysiological level. Future studies should focus on the neurophysiological processes during the transition time when a participant is just starting to experience a feeling of illusory hand ownership. These initial processes during onset of the RHI might differ from the processes occurring during maintenance of the illusion which are captured by most current studies. In line with this, more attention in general should be paid to the time before the onset of the illusion. For example, instead of relying on a separate control condition, data obtained from the trials/events before the onset of the illusion could be compared data obtained from the trials/events after the onset of the illusion. This would avoid confounds induced by control conditions and allow for a better comparison between states of illusion and no illusion.

Further, future studies could make use of the recent developments in combining fMRI and EEG. Combined fMRI-EEG studies can acquire high temporal and spatial resolution at the same time. Such data would allow for a better understanding of the exact processes and the involvement of the various brain areas in the RHI. In addition, this approach would derive EEG and fMRI data from the same RHI setup. Notably, EEG and fMRI studies on the RHI have generally employed different experimental setups and stimulation parameters in the past often due to demands of the specific neuroimaging method. Thus, comparing results across studies has been problematic. A combined fMRI-EEG approach however, would use a single experimental setup for obtaining both, EEG and fMRI data, and thereby allow for direct comparison and integration of these data.

In addition, future studies should strive to ease integration of previous findings with their own results, e.g. by employing previously used parameters and/or measurement standards. This would make results more informative and would reduce the probability of small differences in experimental procedure leading to different results on the neurophysiological level. By adopting a more rigorous and standardised approach, future research will be able to give us a better understanding of the neurophysiological processes underlying illusory hand ownership and body ownership as a whole.

Appendices

Experiment 1: RHI Questionnaire

Please answer each item by marking a number to indicate how much you agree with each statement. Answer all items even if unsure of your answer.

Please call the experimenter if you have any questions.

	Strongly disagree			Neither agree nor disagree			Strongly agree
During the trial it seemed as if I were feeling the touch in the location where I saw the rubber hand touched.	-3	-2	-1	0	1	2	3
During the last trial it seemed as though the touch I felt was caused by the LED light on rubber hand.	-3	-2	-1	0	1	2	3
During the last trial I felt as if the rubber hand were my hand.	-3	-2	-1	0	1	2	3
During the last trial it felt as if my (real) hand were drifting towards the rubber hand.	-3	-2	-1	0	1	2	3
During the last trial it seemes as if I might have more than one left hand or arm.	-3	-2	-1	0	1	2	3
During the last trial it seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand.	-3	-2	-1	0	1	2	3
During the last trial it felt as if my (real) hand was turning rubbery.	-3	-2	-1	0	1	2	3
During the trial it appeared (visually) as if the rubber hand were drifting towards the left (towards my hand).	-3	-2	-1	0	1	2	3
During the trial the rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.	-3	-2	-1	0	1	2	3

Experiment 2 and 3: RHI Questionnaire

Please answer each item by marking a number to indicate how much you agree with each statement. Answer all items even if unsure of your answer.

Please call the experimenter if you have any questions.

	Strongly disagree			Neither agree nor disagree			Strongly agree
During the trial it seemed as if I were feeling the touch in the location where I saw the rubber hand touched.	-3	-2	-1	0	1	2	3
During the last trial it seemed as though the touch I felt was caused by the **Vibration motor under** rubber hand.	-3	-2	-1	0	1	2	3
During the last trial I felt as if the rubber hand were my hand.	-3	-2	-1	0	1	2	3
During the last trial it felt as if my (real) hand were drifting towards the rubber hand.	-3	-2	-1	0	1	2	3
During the last trial it seemes as if I might have more than one left hand or arm.	-3	-2	-1	0	1	2	3
During the last trial it seemed as if the touch I was feeling came from somewhere between my own hand and the rubber hand.	-3	-2	-1	0	1	2	3
During the last trial it felt as if my (real) hand was turning rubbery.	-3	-2	-1	0	1	2	3
During the trial it appeared (visually) as if the rubber hand were drifting towards the left (towards my hand).	-3	-2	-1	0	1	2	3
During the trial the rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.	-3	-2	-1	0	1	2	3

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