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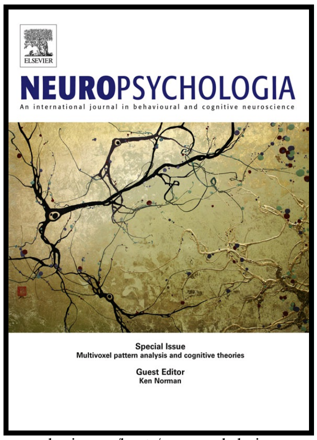

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Experimentally Induced Limb-Disownership in Mixed Reality

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ABSTRACT

The seemingly stable construct of our bodily self depends on the continued, successful integration of multisensory feedback about our body, rather than its purely physical composition. Accordingly, pathological disruption of such neural processing is linked to striking alterations of the bodily self, ranging from limb misidentification to disownership, and even the desire to amputate a healthy limb. While previous embodiment research has relied on experimental setups using supernumerary limbs in variants of the Rubber Hand Illusion, we here used Mixed Reality to directly manipulate the feeling of ownership for one's own, biological limb. Using a Head-Mounted Display, participants received visual feedback about their own arm, from an embodied first-person perspective. In a series of three studies, in independent cohorts, we altered embodiment by providing visuotactile feedback that could be synchronous (control condition) or asynchronous (400ms delay, Real Hand Illusion). During the illusion, participants reported a significant decrease in ownership of their own limb, along with a lowered sense of agency. Supporting the right-parietal body network, we found an increased illusion strength for the left upper limb as well as a modulation of the feeling of ownership during anodal transcranial direct current stimulation. Extending previous research, these findings demonstrate that a controlled, visuotactile conflict about one's own limb can be used to directly and systematically modulate ownership – without a proxy. This not only corroborates the malleability of body representation but questions its permanence. These findings warrant further exploration of combined VR and neuromodulation therapies for disorders of the bodily self.

KEYWORDS
Body Ownership, Disownership, Virtual Reality, Neuromodulation, Xenomelia, Mixed Reality

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AUTHOR CONTRIBUTIONS
Original Paradigm: OK, ET; Experimental Design: all authors; Data Collection: ET, OK; Data Analysis: all authors; Manuscript Preparation: all authors

1. INTRODUCTION

The foundations of our "selves", and our understanding of who we are, are laid by the continuous and successful integration of multisensory information about our body. This interdependence between "mind" and body has occupied the thoughts of scholars time and again: from Descartes' notion that the self cannot exist without the senses (Descartes and Cottingham, 2013), to Husserl positing that there is no possibility of distancing the self from the body or the body from the self (Husserl, 2002), to William James' oft-cited claim that the body is "always there" (James, 1890). There is an overwhelming sense that the direct neural representation of our bodies, in harmony with our actual body composition, forms the basis of an infallible bodily self. However, clinical examples challenge this notion and have suggested that the body indeed can be experienced as lost, not under control, or not belonging (Brugger and Lenggenhager, 2014). This latter feeling of ownership is argued to be a key aspect of our sense of a bodily self (Blanke, 2012). Yet, while psychological and neuroscientific research has extensively investigated the fundaments of the feeling of ownership for a foreign body part, the loss of ownership has largely been neglected.

Empirical insights into corporeal awareness stem to a large extent from experimental designs, which allow temporarily altering the sense of ownership through multisensory stimulation (Botvinick and Cohen, 1998; Ehrsson, 2007; Lenggenhager et al., 2007; Petkova and Ehrsson, 2008). Most famously, Botvinick and Cohen induced illusory ownership of an artificial hand by stroking a rubber hand placed in front of the participant in synchrony with the participant's real hidden hand (Botvinick and Cohen, 1998). This phenomenological experience of ownership over the rubber hand is accompanied by objectively-measurable changes in a broad variety of processes ranging from basic physiological mechanisms (e.g., body temperature (Macauda et al., 2015; Moseley et al., 2008), nociception (Hansel et al., 2011; Romano et al., 2014), cardiac signalling (Park et al., 2016), neural or skin response to threat (Ehrsson et al., 2007), and immunological responses (Barnsley et al., 2011)) up to high-level cognition (see e.g. (Maister et al., 2015) for a recent review). These data thus suggest that the bodily self is highly plastic and based upon momentary sensory integration.

Next to advancing our understanding of the nature of bodily self-consciousness and its disorders, such empirical evidence might contribute towards developing methods to restore the bodily self where it is disturbed (Moseley, 2007; Pazzaglia et al., 2016). Strikingly however, most studies using multisensory stimulation in healthy participants or patients targeted the manipulation to bodily ownership of an additional and external, fake or virtual body (part), someone else's limb (Hohwy and Paton, 2010), or more recently, two virtual representations of one's own limb (Newport and Preston, 2011; Ratcliffe and Newport, 2017). In the above-described rubber hand illusion (RHI), the most striking phenomenological perception is the feeling of ownership for the supernumerary rubber hand not the feeling of disownership for the real hand, which has generally been reported to be rather low (e.g. (Longo et al., 2008)). Furthermore, implicit measures of the illusion have shown to be predicted by the feeling of ownership for the rubber hand rather than by the feeling of disownership (Folegatti et al., 2009). In fact the two sensations are generally difficult to disentangle due to the nature of the RHI's experimental design (Longo et al., 2008), and thus call for direct experimental manipulation of disownership (Folegatti et al., 2009).

An experimental paradigm directly probing disownership is especially important from a clinical perspective. Body ownership disturbances after brain damage range from the feeling of one's limb not being there (asomatognosia, cf. (Jenkinson et al., 2018)), to a sensation of disownership combined with feeling of hatred towards it (misoplegia, cf. (Loetscher et al., 2006)) or attribution of ownership to another person (Bottini et al., 2002), to the pathological embodiment of another person's hand (cf. E+ patients (Garbarini et al., 2015)). The latter is phenomenologically closest to what participants report during the RHI. However, these cases are quite rare (Fossataro et al., 2018), whereas the pure feeling of disownership (accordingly named E-) prevails after right hemispheric brain damage. This is also the case for various psychiatric conditions such as depersonalization syndrome, in which the own biological body often does not feel like belonging to the "self" anymore (Sierra et al., 2005). Perhaps the purest sense of body disownership manifests in individuals suffering from xenomelia. These individuals feel like parts of their body do not belong to them (McGeoch et al., 2011) often resulting in extensive pretending behaviour (i.e. simulating their desired body state) and the desire for amputation (Brugger et al., 2013). Individuals with clinically altered body ownership for their biological body typically show enhanced illusory ownership in RHI-like setups (e.g. (Lenggenhager et al., 2015; Smit et al., 2018; van Stralen et al., 2013)) which might suggest a stronger influence of online sensory information over longer term body representation. This further highlights the need for an experimental protocol to directly induce and measure disownership of the real body. Such paradigms are important to better understand and disentangle multisensory mechanisms underlying the broad range of clinically altered body ownership symptoms.

We here describe a paradigm, the Real Hand Illusion (ReHI), designed to address this discrepancy between clinical reports and existing research paradigms in trying to alter the sense of ownership of one's own biological limb in a Mixed Reality setup. During the illusion, participants view their own hand directly and from a first-person perspective through a head-mounted display (HMD) being touched either synchronously or asynchronously to the visual feedback (see Figure 1). The paradigm extends the study by Gentile and colleagues (Gentile et al., 2013), as it allows participants to view and move their own hands in the virtual space in real-time, eliminating the perception of viewing pre-recorded feedback. As the setup is fully automated possible confounds due to manual synchronization are precluded. The illusion was assessed, immediately after each condition, using a questionnaire adapted from the classical RHI questionnaire (Botvinick and Cohen, 1998; Longo et al., 2008). As synchronous visuotactile stimulation has repeatedly been shown to increase perceived ownership, we predicted continued ownership during synchronous stimulation and – more pertinent to the phenomenology described in clinical cases – decreased ownership of the own limb during asynchronous stimulation (Gentile et al., 2013). The latter could thus be regarded as temporarily mimicking the phenomenology found in Somatoparaphrenia or Xenomelia patients, i.e. the feeling of estrangement for their own limb.

Both Somatoparaphrenia and Xenomelia have been suggested to relate to alterations in multisensory bodily areas in the predominantly right-hemispheric posterior parietal areas (Hilti et al., 2013; McGeoch et al., 2011; Rode et al., 1992) as well as structural and functional hyper-connectivity within the sensorimotor system (Hänggi et al., 2017). As a consequence, both syndromes predominantly affect the left side of the body. In a second study, we thus investigated whether the feeling of disownership could be evoked more easily on the left as compared to the right hand in healthy participants. Based on previous literature on the rubber hand illusion which suggests stronger illusion for the left hand (Ocklenburg et al., 2011), we hypothesized a stronger sensation of disownership during asynchronous stroking of the left as compared to the right hand.

In line with the idea of a right posterior parietal involvement in disorders of body ownership, we further investigated whether neuromodulation of these parietal areas might alter the illusion in a systematic way. Brain imaging studies in individuals with Xenomelia have reported altered neural processes in the superior and inferior parietal lobe (Hilti et al., 2013; McGeoch et al., 2011; Oddo-Sommerfeld et al., 2018) at least partly overlapping with the network described by Gentile and colleagues (2013). Limb misidentification due to right-hemispheric damage has also been associated with parietal areas (Antoniello and Gottesman, 2017; Vallar and Ronchi, 2009). In line with this, neuromodulation through vestibular stimulation, which activates right parieto-insular areas (Lopez et al., 2012), has been shown to be helpful in Somatoparaphrenia (Rode et al., 1992) and consecutively also suggested as a therapeutic approach for Xenomelia ((Ramachandran and McGeoch, 2007); but see also (Lenggenhager et al., 2014)). Similarly, left anodal galvanic vestibular stimulation has been used to manipulate bodily ownership in healthy participants in a rubber hand illusion setup (Lopez et al., 2010). In a further, exploratory study, we used transcranial brain stimulation rather than indirect peripheral stimulation to alter activation of right parietal areas. We applied anodal and cathodal tDCS over the right superior parietal lobe normalised by a baseline sham stimulation. In line with previous literature we expected stimulation of right parietal networks to modulate body ownership. This hypothesis is further supported by two recent tDCS studies reporting a modulation of the drift measure of the RHI in case of anodal stimulation applied over the right temporo-parietal junction (and right pre-motor cortex (Convento et al., 2018) and a change in the onset time of the illusion, but not drift, during anodal stimulation over right posterior parietal cortex (PPC) respectively (Lira et al., 2018). These studies further reported significant, if slightly different, effects of anodal tDCS on perceived body ownership.

2. MATERIALS AND METHODS

2.1. Setup

The technical setup follows the methods of our previous study (Bernal et al., 2016) as described in the following. A MacBook Pro Retina by Apple (Apple Inc., Cupertino, CA, USA), was used to render the visual feedback. The laptop had a dedicated AMD Radeon R9 M370X graphics card. The Oculus Rift DK2 (Subsidiary of Facebook, Menlo Park, CA, USA), Version 1.6 (SDK 0.5.0.1), was used to display the feedback. The HMD has a resolution of 960x1080pixels per eye, a horizontal field of view of 100°, and a refresh rate of 60Hz. Head orientation but not translation was tracked, as participants were asked to keep their head stationary during each trial. A LeapMotion controller (Leap Motion, Inc. San Francisco, CA, USA, Software Version 2.3.1) recorded the participant's hand as well as the paintbrush, used to provide tactile feedback, using the integrated infra-red (IR) cameras. The visual stimuli used the resulting IR pass-through feed so that participants would see their own hand, as opposed to a rigged 3D model (cf. supplemental figure 1). Finally, the Unity game engine (Unity Technologies, San Francisco, CA, USA Version 5.1.3f) was used to render the stimuli in an otherwise empty virtual space.

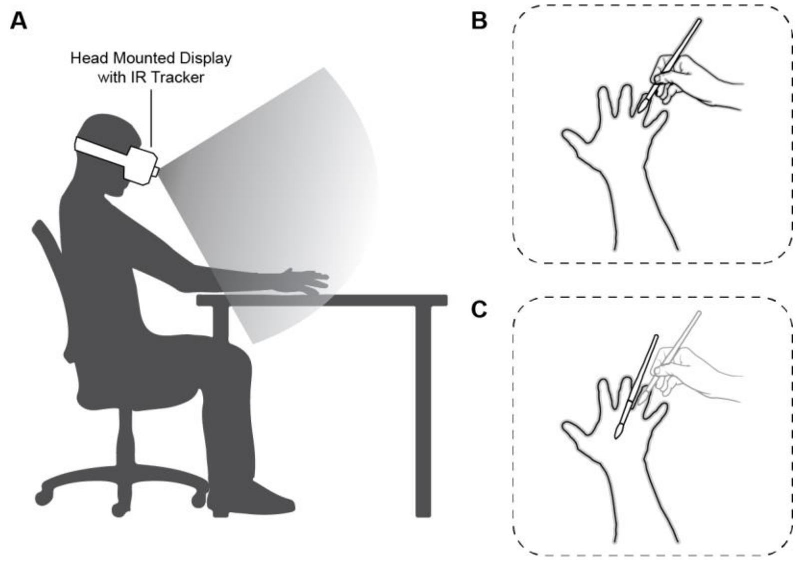

Figure 1 – A. Participants are seated at a desk with their right arm resting on a pillow at their side. They wear the Head-Mounted Display with attached IR camera. The video feed of the camera is used to display the image of the participant's own hand in the HMD. B. The biological and augmented limbs are aligned so that participants see their own hand in the correct anatomical position. In the control condition the feedback accurately presents the experimenter's hand and the paintbrush providing synchronous (matching) visuotactile feedback. C. In the experimental condition, a 400ms delay is introduced in the visual feedback. Participants therefore feel the touch of the paintbrush (light grey) before seeing the paintbrush in the corresponding position.

2.2. Synchronous and Asynchronous Feedback

In order to change the delay of the visual feedback between the synchronous and asynchronous conditions, a buffer of the IR-feed was implemented using Leap's Controller object within Unity. This maintains a frame history buffer of 60 frames. At 120fps sampling of the LeapMotion cameras, this provides up to half a second delay. Here, a 40-frame delay was used in order to produce a ~400ms delay during asynchronous feedback. This includes the intrinsic latency of the equipment which is as follows: tracking camera frame rate (120fps, ~8ms), tracking algorithm (4ms), display refresh rate (60Hz, ~17ms), and GPU calculations (~17ms) totalling to an intrinsic system delay of ~46ms (Bernal et al., 2016). Feedback in the synchronous condition was therefore achieved in under 50ms. The (intrinsic) delay in the synchronous feedback condition was therefore well below the temporal mismatch threshold shown to interfere with visuotactile integration (300ms, Shimada et al., 2009), whereas it was well above this threshold in the asynchronous condition.

2.3. Tactile Feedback

Tactile feedback was provided using an ordinary flat, short-haired paint brush (size 10). The experimenter stroked the dorsum of the participant's hand and fingers in different positions and directions for a total of three minutes. Unlike in previous limb ownership studies, only the participant's hand was stroked, as opposed to an additional rubber hand. Accordingly, the visuo-tactile conflict in the asynchronous condition is purely temporal, and the visuo-tactile feedback in the synchronous condition exactly matches the actual stimulation. It should be noted that the experimental condition of the RHI, synchronous feedback, is in this case the control condition, Figure 1B; the asynchronous visuotactile stimulation, the control condition in the RHI, becomes the experimental condition, Figure 1C.

In studies 2 and 3, but not study 1, the three-minute illusion was preceded by one minute of synchronous, visual only, feedback. Here, participants were asked to move their hands in order to familiarise themselves with the environment, get accustomed to the feedback, and appreciate that they have full control of their own arm in the VR space.

2.4. ReHI Questionnaire

Following each experimental block, participants were asked to write down any comments they had about their perception of the illusion (open feedback). Phenomenological aspects of the illusion were then systematically assessed with a questionnaire adapted from the classical RHI questionnaire (Botvinick and Cohen, 1998; Longo et al., 2008) using a banded visual analogue scale (Matejka et al., 2016). Questions one through six were scored positively from 0 to 10, whereas questions seven through ten pertain to the feeling of disownership and were therefore reverse-coded for the analysis (0 -> 10, 1 ->9, etc.). This was done so that all ten questions were combined to calculate an overall illusion-score with a possible range of 0 to 100. A score of 100 represents the highest possible 'embodiment score', whereas a score of 0 would reflect a complete loss of ownership and agency of the seen hand.

2.5. Participants

Study 1 (N=20, age μ=21±1years, 12 female) investigated the illusion based on the individual questions and an overall score (see figure 2 for boxplots). A t-test comparing the illusion score between the two conditions of interest (i.e., synchronous versus asynchronous stroking) revealed a significant effect ($t(19)=4.58$, $p<0.001$, Cohen's dz = 1.02) between conditions. This Cohen's d was used for power calculations in studies 2 and 3. Participants for all three studies were right-handed (self-reported) and had normal or corrected to normal vision.

A power calculation (G*Power (Faul et al., 2007)) indicated that a sample size of 15 would be required to detect an effect size of dz = 1.02, with the alpha level set at .05, with power of .95 (two-tailed). Twenty participants were recruited for study 2 (age: μ=21.55±2.48years, 10 females).

Power calculation for the exploratory neurostimulation study was further informed by Kammers and colleagues effect size of approximately d = 0.6, reported in their rTMS study on the RHI (Kammers et al., 2010). Using a paired samples t-test to contrast two stimulation conditions, to reach 80% power with this effect size (alpha level = .05) would require 24 participants. Twenty-six participants (age μ=21.32±8.31years, 16 male) were recruited and completed the tDCS paradigm (study 3). All participants refrained from consuming caffeine for at least three hours prior to the tDCS stimulation. All studies had been approved by the University of Central Lancashire's Ethical committee (Protocol PSYSOC336).

2.6. Transcranial direct current stimulation

TDCS over the right superior parietal lobule (SPL) was used to change cortical excitability (see Figure 3). In one condition, anodal stimulation was applied over the right SPL with the aim of increasing cortical excitability, with the cathodal electrode as the reference. In another condition, cathodal stimulation was applied over the right SPL with the aim of decreasing cortical excitability. The third condition was the sham stimulation condition, which acted as a baseline against which to compare active stimulation. Participants attended two separate sessions, separated by at least three days.

Participants always completed the anodal and cathodal stimulation conditions in separate sessions, to avoid after-effects from one condition affecting another condition. Half the participants additionally completed the sham condition at the start of the first session, while the remaining half completed the sham condition at the start of the second session. The stimulation was applied double-blinded using pre-determined codes stored on the tDCS equipment, which determined the type of stimulation applied (anodal, cathodal or sham) without the experimenter's knowledge.

The electrodes were positioned with the aid of an EASYCAP 21 EEG cap (EASYCAP, Herrsching), with the scalp electrode positioned over the P4 region according to the international 10-20 system. The P4 electrode is located approximately over the right superior parietal lobe (Herwig et al., 2003) and has previously been used to target this region (Lira et al., 2018; Ono et al., 2016). The reference electrode was positioned over the ipsilateral shoulder, held in place with a rubber strap (cf. Figure 3).

In the two tDCS conditions, participants received 1200s (including 8s of fade-in and 8s of fade-out) of tDCS, using a NeuroConn DC-Stimulator Plus (NeuroConn, Germany). A 1.5mA current was delivered through 25cm^2 saline-soaked sponges (0.9% NaCl solution), held in place on the participant's scalp by rubber straps (current density of 0.06mA/cm^2). Stimulation was applied for 600s before task onset, and continued 600s after task onset.

Sham stimulation consisted of stimulation applied for 38s, before dropping to regular pulses of 115μA (lasting 3ms) every 550ms, which gives an average current strength of 0.002mA. This level of stimulation is far lower than required to cause changes in cortical excitability but allows monitoring of impedance (which could indicate poor electrode contact or disconnection).

2.7. Analysis and Data Availability

Paired frequentist and Bayesian t-tests were conducted in JASP (JASP Team, 2018). These tests were two-tailed for NHST and directional for calculation of BF due to clear directional hypothesis of the illusion effect.

Significance thresholds were set to $p<.05$ and $BF>3$ ($BF<.3$) respectively. NHST was used in combination with power-calculations; Bayesian statistics (Dienes, 2014) are included as potential evidence in favour of the null. Cronbach's alpha was calculated in R using R-Studio (R Development Core Team, 2017) and the Psych package (Revelle, 2017). All data are available to the readers via a public Open Science Framework project (http://osf.io/wbp59).

Figure 2 – Questions and box plot with interquartile ranges of the results across the three studies (C-Control, I-Illusion) – Questions 1 through 6 were adapted from previous studies on the RHI. Question 4 is a control question and question 5 addresses participants' sense of agency. Questions 7 through 10 were included to directly address disownership aspects of the ReHI. Participants in all three cohorts rated embodiment higher given synchronous visuotactile feedback about their upper limb in the control condition compared to the asynchronous feedback during the ReHI. All asterisks indicate NHST significance. Data for S2 and S3 (sham stimulation) are taken from left hand.

3. RESULTS

As this is a novel experimental setup, we first set out to investigate the effects of the Real Hand Illusion on the phenomenology of the bodily self, focusing on hand ownership (Q1), location of touch (Q2-3), agency (Q5), and aspects of disownership (Q7-Q10). To compare the overall illusion across conditions, a combined score was created based on all questions; for this, disownership questions were reverse-coded, leading to a possible range of scores from 0 to 100.

3.1. Study 1 – Limb Disownership

In study 1, twenty participants completed the synchronous and asynchronous feedback conditions and the ten-item questionnaire. Individual questions and results across all 3 studies are illustrated in Figure 2. As hypothesised, participants rated the questions significantly more positively in the control condition (77.53±13.08) than during the illusion (58.47±17.27, $p<.001$, BF=292.66) designed to induce a loss of ownership.

To highlight a few key questions: participants rated the seen hand to feel less like their own during the illusion (Q1 control: 7.58±3.21 to illusion: 4.46±3.21 ($\mu\pm\sigma$), $p=.002$, BF=36.50); similarly, they reported that it felt less likely that the stroking they felt on their hand was due to the stroking on the seen hand (Q2: 7.06±3.44 to 4.16±3.46, $p=.009$, BF=10.96), and less likely that it was stroked in the same location (Q3: 8.87±1.47 to 3.85±3.51, $p<.001$, BF=2425.24). Participants also reported an effect of the ReHI on their (hypothetical) ability to move the seen hand ("feeling of agency" Q5: 8.81±2.11 to 7.16±3.37, $p=.021$, BF=5.41). With respect to the disownership questions, participants reported that their hands felt less vivid than normal during the illusion (Q10: 6.83±2.88 to 5.15±2.95, $p=.016$, BF=6.89). Questions Q7-9 were not rated significantly differently between conditions in study 1 but may be worth further investigating as indicated by the inconclusive BF (all $p>.085$, all BF inconclusive .45<BF<.1.75).

3.2. Study 2 – Lateralisation

In study 2, the lateralization of body representation and its malleability were investigated. It was hypothesised that the strength of the illusion would be higher for participants' left hand compared to their right. A 2 x 2 repeated measures ANOVA, based on the overall illusion strength, confirmed our data from study 1 with respect to the main effect of the illusion. The total score significantly dropped from 83.95±13.10 during synchronous feedback to 66.36±20.06 during the asynchronous feedback of the illusion (main effect of illusion $F(1,19)=16.04$, $p<.001$, $\eta^2=.46$). There was no overall effect of laterality ($p=.107$); however, there was a significant interaction between the two factors ($F(1,19)=5.84$, $p=.026$, $\eta^2=.24$): Questionnaire scores were lower for the left than the right hand during the illusion but not in the control condition. As hypothesised, the illusion was stronger for the left hand (paired t-test: μ-difference: 6.41±2.69, $t(19)=2.38$, $p=.028$) . The ANOVA results were corroborated in Bayesian t-tests. The data strongly support a main effect of illusion (C>I: BF=92.98) but not of lateralization (R≠L, BF=.78). The interaction, indicated by the left-right differences in both conditions, was also supported by the data (RI-LI > RC-LC: BF=4.61), resulting from the lateralisation difference during the illusion (LI < RI: BF=4.43).

3.3. Study 3 – Neurostimulation

In study 3, we set out to investigate the involvement of right parietal networks in maintaining body representation during the Real Hand Illusion. In two separate sessions, participants completed the ReHI while receiving sham, anodal, or cathodal tDCS stimulation, with the scalp electrode placed over the right superior parietal lobe. As this was an exploratory study, we were mainly interested in the overall effect of stimulation on ReHI score and the main contrast of anodal versus cathodal stimulation. In order to normalise the data, we therefore subtracted the average ReHI score during sham stimulation from anodal and cathodal scores. This resulted in a 2 x 2 repeated measures design with factors Illusion (synchronous, asynchronous) and Stimulation (anodal, cathodal). In-line with the studies 1 and 2, we report a significant main effect of the illusion in a third, independent participant pool ($F(1,25)=25.54$, $p<.001$, $\eta^2=.51$, $BF_{C>I}=1474.21$). We additionally observed a main effect of Stimulation with ReHI scores being higher during cathodal stimulation than during anodal stimulation ($F(1,25)=5.35$, $p=.029$, $\eta^2=.18$, $BF_{C>A}=3.81$, $BF_{C\neq A}=1.94$, see Figure 3b), although there was no interaction between illusion condition and stimulation condition ($F(1, 25) = 0.02$, $p = .89$).

3.4. Questionnaire Reliability

As this is a novel paradigm accompanied by a newly designed questionnaire, we ran a reliability analysis across the three data sets (N=66) – once for the control condition, and once for the illusion condition. Cronbach's alpha for the questionnaire responses in the control condition was $\alpha_{control}=0.79$, in the illusion $\alpha_{illusion}=0.85$, indicating good internal consistency across the three cohorts.

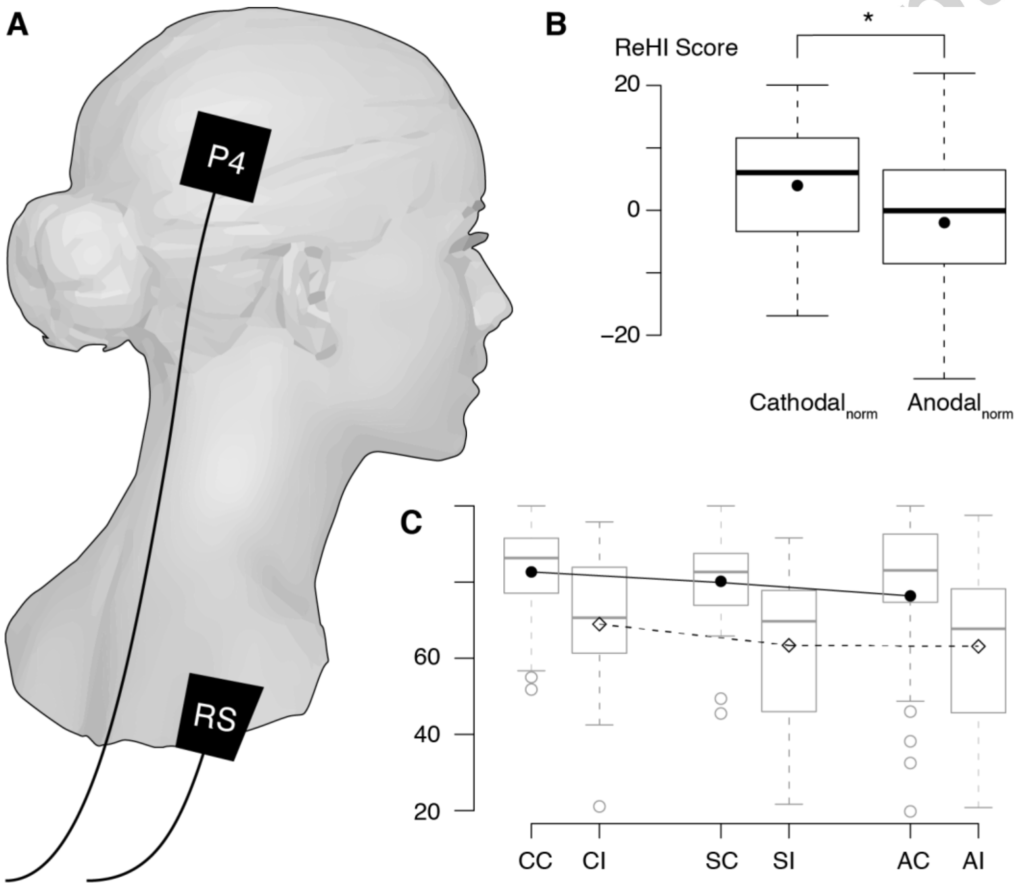

Figure 3 Effects of Transcranial Direct Current Stimulation on ReHI Strength. A Electrodes were placed on the P4 position based of the international 10-20 system and the right shoulder. B The main contrast indicates that anodal stimulation over P4 significantly decreased embodiment across both conditions compared to cathodal stimulation. (Sham scores were subtracted for baseline correction.) C Breakdown of questionnaire scores across control and ReHI conditions and stimulation type. All boxplots indicate medians and Interquartile ranges; means are indicated by solid circles or diamonds (CC/CI = Cathodal Control/Illusion; SC/SI = Sham Control/Illusion; AC/AI = Anodal Control/Illusion).

4. DISCUSSION

We here introduce a body-illusion that directly reduces the feeling of ownership over one's biological limb without relying on feedback from a supernumerary proxy such as a rubber hand. Participants view their own arm, in Mixed Reality, from an embodied, first person perspective but receive feedback that contains a temporal, visuotactile conflict. In a series of three studies, in three separate participant pools, we demonstrate that the asynchronous feedback in the Real Hand Illusion causes participants to rate ownership (and the sense of agency) over their own hand and related sensations significantly lower than in the synchronous control condition. In addition, a number of participants independently reported a phenomenon akin to "pins and needles", the tickling sensation that often occurs after transient paraesthesia.

The Real Hand Illusion, which could be considered as an inverse of the classical rubber hand illusion, hence modulates body ownership by introducing a controlled mismatch into bottom-up multisensory integration. Our data suggest that this weakened embodiment is pronounced for the left hand, supporting the right hemispheric dominance hypothesis of body representation as reflected in neuropsychological case reports and previous ownership illusion studies in healthy participants. Transcranial direct current stimulation over the right superior lobule modulated the overall strength of limb ownership, corroborating the role of right posterior parietal networks for multisensory representations of the body and self.

4.1. Phenomenology

Embodiment, ownership, and the sense of agency have been argued to be matters of "a very thin phenomenal awareness" (Gallagher, 2007) and to only form the "background of mental life" (Longo et al., 2008). Often, we only fully become aware of these processes when they break down – which can have severe consequences (see e.g. Ananthaswamy, 2016; Sacks, 1998). While research into the sense of agency has managed to address this by experimentally modulating a loss of control (Franck et al., 2001; Kannape and Blanke, 2013; Leube et al., 2003a, 2003b; Nielsen, 1963; Wegner, 2002), a symptom that is often evident in clinical conditions (see e.g. Blakemore et al., 2002), ownership studies have instead investigated the opposite: a 'positive' ownership of an artificial limb such as a rubber hand (Botvinick and Cohen, 1998) or rubber foot (Lenggenhager et al., 2015), someone else's filmed arm (Hohwy and Paton, 2010) or even two versions of one's own hand (Ratcliffe and Newport, 2017) in-line with the E+ but not E- patients described in the introduction (Garbarini et al., 2015). Analog to sensorimotor studies delineating the spatiotemporal limits of agency, we have here introduced a paradigm to directly induce disownership of one's own limb: where participants report a loss of control over their actions in agency research, participants in the ReHI perceive a significantly weakened ownership over their own hand and arm, along with the spontaneously reported sensation of pins and needles.

The topic of disownership is a somewhat contentious area with respect to the RHI. There is a general consensus that the rubber hand is embodied during synchronous feedback (see e.g. Serino et al., 2013) – arguably only into the body image (for perception) but not the body schema (for action) (Kammers et al., 2009). However, this does not automatically imply that one's own limb is simultaneously disembodied. While arguments have been made for some disownership and deafferentation, either by asking directly about disownership of the real hand (Preston, 2013) or by inferring from physiological data (drop in skin temperature (Moseley et al., 2008; Salomon et al., 2013) or alterations in immune response (Barnsley et al., 2011), but see (de Haan et al., 2017) for a critical account), evidence suggests that multiple representations of the hand might co-exist (Ehrsson, 2009; McGonigle et al., 2002) severely limiting the argument made in previous RHI-type studies. This also corresponds to the results and interpretation of Lane and colleagues (2017) who specifically targeted limb disownership during the RHI: disownership for the biological limb is less robust than ownership for the rubber hand, as attention is primarily directed at the latter. Ultimately, the strongest statement to be made in favour of disembodiment from these previous paradigms is that the supernumerary hand replaces or "functionally suppresses" the participant's actual hand (Longo et al., 2008).

Another important argument raised by Longo and colleagues in their psychometric approach to the RHI is that the asynchronous condition cannot be reduced to a mere control condition. Sensations grouped under the umbrella term "deafference", only occur in the asynchronous condition (and still rely on a weak embodiment of the rubber hand). The ReHI illusion targets exactly these aspects of body disownership but based on the (strongly embodied) biological limb of the participant. Sensations such as "numbness" and "pins and needles", included as direct questions in both conditions in Longo et al., were spontaneously reported by the participants in all three cohorts of the ReHI – and only in the asynchronous and in this case illusion condition. Further, the feeling of disownership and deafferentation are both enhanced during asynchronous stroking.

In summary, the phenomenology of the ReHI extends previous findings as it precludes both supernumerary embodiment and the replacement of the actual limb representation. There is only one arm. Rather than being indicative of a malleability to multisensory body illusions or an ability to incorporate supernumerary limbs, the current findings hence suggest that limb representation can directly be attenuated and phenomenologically deafferented, without "tricking the brain" by including a proxy. It is therefore not so much illustrating the malleability of limb representation but questions its actual permanence: contradicting William James famous premise (James, 1890), the body may not always be there.

4.2. Handedness and Lateralisation

Study 2 illustrates that the phenomenological experience of the ReHI was stronger for the left hand as opposed to the right. This difference in lateralisation was specific to the illusion condition as no lateralisation was observed in the control condition. The findings are in line with mounting evidence that Xenomelia, similar to Somatoparaphrenia, more often than not affects the left side of the body (Brugger and Lenggenhager, 2014; McGeoch et al., 2011). While an argument is to be made that lateralisation may be a result of handedness, and stronger bodily illusions have been reported for the non-dominant hand (Brugger and Meier, 2015), evidence from the RHI suggests there is a right-hemispheric dominance for sense of body ownership independent of handedness ((Ocklenburg et al., 2011), but also see (Smit et al., 2017)). Taken together, this suggests that the ReHI is mediated by multisensory bodily areas in right-hemispheric posterior parietal areas (Hilti et al., 2013; McGeoch et al., 2011; Rode et al., 1992), further motivating the exploratory neurostimulation study to focus on the left upper-limb.

4.3. Neurostimulation modulates Limb Disownership

The results from Study 3 indicated that application of tDCS over the right SPL modulated the experience of ownership, dependent on the polarity of stimulation. Specifically, anodal stimulation led to reduced feelings of ownership over the limb, while cathodal stimulation increased feelings of ownership. It should be noted that this was an exploratory study, aiming to link the ReHI to activity in the parietal cortex; future studies should therefore aim to test under which conditions the effect of stimulation holds. Our data suggest that transcranial stimulation affected the experience of ownership during both the illusion and control conditions, suggestive of a broad effect of stimulation that is not dependent on synchronous visuotactile feedback. This is in line with two recent neurostimulation studies reporting mainly non-illusion-specific effects of anodal stimulation over right PPC (Convento et al., 2018; Lira et al., 2018).

An open question remains as to the exact mechanisms affected by neurostimulation. Convento and colleagues (2018) report the strongest effect of stimulation on the drift measure rather than the subjective strength of the illusion, whereas Lira and colleagues (2018) report a stimulation-dependent change in illusion-onset times. In the latter study, the authors argue that the observed differences may be due to generally enhanced multisensory processing; in the former, the authors further discuss the involvement of body-specific sensory integration (see also (Tsakiris et al., 2008)). What both of these previous studies have in common, however, is that anodal stimulation of the parietal lobe led to increased efficacy of the illusion (i.e. faster time to illusion onset, or proprioceptive drift) – that is, participants perceived *more* ownership over the rubber hand – whereas, in the present study, a similar stimulation paradigm resulted in participants perceiving *less* ownership over their own arm. Although these results may seem somewhat contradictory, they can be reconciled, if we assume the effect of stimulation in both the RHI and ReHI is relevant to inducing disownership over one's own limb. The underlying mechanism of this effect could on the one hand relate to a localized change in multisensory processing (Lira et al., 2018), body-specific integration (Convento et al., 2018; Tsakiris et al., 2008), or a re-weighting of sensory information over body-representation in the parietal lobe, or on the other hand a change in functionally connected regions such as the primary or secondary somatosensory cortex (Hänggi et al., 2017), where structural and functional hyper-connectivity have been reported in individuals with Xenomelia. This explanation is necessarily speculative but could further be investigated using neuroimaging alongside the ReHI paradigm.

From a clinical perspective, it is further of interest that previous studies have shown that transcranial magnetic stimulation (TMS) applied to the right temporoparietal junction (TPJ) disrupts the rubber hand illusion for body-like objects (but not other objects, cf. Tsakiris et al., 2008). Clinically, low-frequency repetitive TMS applied to the TPJ may decrease the frequency of auditory hallucinations in patients with a diagnosis of schizophrenia, a symptom frequently linked to loss of agency or ownership over self-generated speech (Moseley et al., 2013; Slotema et al., 2014). Taken together, these findings suggest that non-invasive neurostimulation is capable of affecting the perception of bodily ownership and support the therapeutic potential of neurostimulation in disorders of bodily ownership.

4.4. ReHI Considerations

In contrast to the on-going, artificially synchronised visuotactile feedback required by the RHI, the ReHI relies on exploiting the same bottom-up multisensory integration processes by introducing a temporal mismatch to disrupt body ownership. In addition to the aforementioned conceptual advantages, this has a number of practical advantages. One, the sensation of the mismatch is immediate. Unlike the RHI, which relies on continued synchronous feedback from two distinct, visuotactile sources and has reported onset times between 10-50 seconds (Ehrsson, 2004; Kalckert and Ehrsson, 2017) the ReHI relies on a hard-coded temporal mismatch from a single source. Two, the multisensory mismatch is unresolvable, making the illusion very stable. Participants feel the touch on the back of their hand before receiving visual feedback. As the position of the subsequent touch-location is unpredictable, there cannot be an adaptation to the conflicting sensory information. Three, the mismatch is purely temporal. Whereas inadvertent spatiotemporal incongruencies occur in both synchronous and asynchronous conditions in the RHI (and to a lesser extent in Gentile et al., 2013), only a single hand is stimulated in the ReHI. Four, and continuing this point, the control condition is very accurate, as the perceived location of the touch exactly corresponds to the seen location. The technical setup precludes an unwanted (spatial) mismatch, apart from the intrinsic (temporal) delay.

While previous (Mixed Reality) studies mainly used RHI-type setups (IJsselsteijn et al., 2006; Shimada et al., 2009) and thus still relied on an albeit virtual proxy, some have used similar visual feedback based on the participant's own body (Suzuki et al., 2013), or overlapped feedback from a virtual or someone else's real hand over the participant's hand (Hohwy and Paton, 2010; Yuan and Steed, 2010). However, these studies only matched individual aspects of the current setup but differed with respect to at least one of the four constraints for the (body-) integration of multisensory signals described by Blanke and colleagues (2015): correct proprioceptive (1) and body-related visual information (2), adherence to peripersonal space (3), and continued congruence of multisensory feedback (4). Our setup further extends the setup used by Gentile and colleagues (2013) as it allows for real-time manipulation. Finally, the setup is portable and easily implemented, making it a promising tool for clinical studies and potential outpatient treatment. The paradigm relies on a simple (video) buffer, making it adaptable to a range of mobile devices and commercially available research platforms.

4.5. Limitations and Future Directions

There are still a number of open questions to address. For example, we based our questionnaire on widely used RHI items but included four new questions directly addressing limb disownership (Q7-10), extending the questionnaire used in (Gentile et al., 2013). A follow-up study that investigates an expanded questionnaire using principal component analysis, similar to the approach taken by Longo and colleagues (Longo et al., 2008) may be able to improve the reporting of the phenomenology of the ReHI. Linking back to the “pins and needles” sensation spontaneously reported by participants, physiological reactions to the illusion should be investigated. Gentile and colleagues (2013) have illustrated changes in galvanic skin conductance depending on the disembodiment of the shown hand. Further studies may follow previous protocols on the RHI to investigate body temperature (Macauda et al., 2015; Moseley et al., 2008), nociception (Hansel et al., 2011; Romano et al., 2014), cardiac signalling (Park et al., 2016), and immunological responses (Barnsley et al., 2011)) up to high-level cognition (Maister et al., 2015).

A further line of inquiry should address the clinical aspects of limb disownership by working with patient populations. For example, individuals with Xenomelia show an enhanced response for the affected limb in a rubber hand illusion type of setup (Lenggenhager et al., 2015). Does the same hold true for the ReHI and how does its phenomenology compare to the sensation of “over-completeness” described by these individuals? Does it capture aspects of loss of limb ownership experienced in Somatoparaphrenia analogous to the RHI in E+ patients (Garbarini et al., 2015)? Applying the ReHI in individuals with Xenomelia may recreate the reported feeling of disownership – or, by inducing disownership over an unwanted limb – create a cessation in the dysphoric feeling of over-completeness. Similar to the pretending behaviour exercised by these individuals (First, 2005; L. Fischer, 2015), this may offer a temporary relief, if not a treatment. Research with such a cohort will further be relevant to understanding the permanence of body representation. If the loss of ownership is a gradual process, it could potentially be tracked longitudinally using the ReHI and further related to the frequency and duration of pretend behaviour over time. The exploratory tDCS results further merit investigation of neurostimulation as a therapeutic possibility (although this may evoke ethical questions pertaining to the identity of individuals with Xenomelia). Finally, applying an analogue paradigm to the full body (Blanke et al., 2015) may provide an experimental link to investigating aspects of depersonalisation in the general population (Sierra and David, 2011).

5. CONCLUSION

The Real Hand Illusion introduced here offers a direct way of modulating limb ownership in healthy individuals. It does so without relying on a proxy, but by introducing a temporal, visuotactile mismatch into bottom-up processed feedback about one's own limb in Mixed Reality. These findings are corroborated by two additional studies in independent participant pools linking the illusion to right posterior parietal networks for multisensory representations of the body and self. By directly investigating the loss of ownership of one's own limb, analogue to research into the sense of agency, the Real Hand Illusion opens up the possibility of more adequately addressing the majority of clinical cases of altered body ownership; further, it provides a novel method of investigating body representation and its permanence in healthy individuals.

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Highlights

- Mixed Reality Illusion induces sense of disownership of biological limb.
- Illusory Disownership is stronger for left limb, in-line with neuropsychological cases.
- Limb-ownership is modulated by transcranial stimulation of right parietal network.
- Results support lateralized right-parietal body network.
- Participants spontaneously report perceiving a "pins and needles" sensation.