



The rubber hand illusion depends on a congruent mapping between real and artificial fingers



Martin Riemer^{a,b,*}, Xaver Fuchs^c, Florian Bublitzky^d, Dieter Kleinböhl^a, Rupert Hölzl^{a,c}, Jörg Trojan^{c,e}

^a Otto Selz Institute for Applied Psychology—Mannheim Centre for Work and Health, University of Mannheim, Germany

^b Aging & Cognition Research Group, German Center for Neurodegenerative Diseases (DZNE), 39120 Magdeburg, Germany

^c Department of Cognitive and Clinical Neuroscience, Central Institute of Mental Health, Medical Faculty Mannheim, Heidelberg University, Germany

^d Department of Psychology, School of Social Sciences, University of Mannheim, Germany

^e Department of Psychology, University of Koblenz-Landau, Germany

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ABSTRACT

The rubber hand illusion (RHI), in which a visible artificial hand is touched (or moves) synchronously with the participant's unseen own hand, indicates that body representations can undergo rapid changes. While several constraints for this illusion have been described, some reports highlight a remarkable flexibility of body representations, even contradicting a priori assumptions regarding body appearance and anatomy (e.g., the subjective embodiment of a third arm).

Here we examine the impact of congruence between touches at (or movements of) the real and the artificial hand, as well as the role of predictability of touches (or movements). We implemented two versions of the RHI paradigm, based on passive tactile stimulation and active voluntary movements.

The results show that (a) predictability does not modulate perceived embodiment, and that (b) congruent mapping between real and artificial fingers is a necessary condition for both the tactile and the motor RHI. Together with previously reported constraints for bodily illusions, these results are reduced to four principles, which determine subjective embodiment: temporal synchrony, congruence of mapping between real and artificial body parts, body unity and body shape.

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1. Introduction

The development of a bodily self (i.e., the conscious perception of 'being' or 'having' a body) is derived from two different aspects concerning the relation between the body and the external world, commonly referred to as body ownership and agency (Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009; Tsakiris, Prabhu, & Haggard, 2006). Body ownership denotes the sense that one's own body is the source of sensations (Tsakiris et al., 2006). External events at the bodily borders are perceived as somatic sensations, which can be described by the notion 'What happens to this body, happens to me'. Agency reflects the fact that phenomenal intentions to modify the external world can only be realized by controlling one's own body movements (Gallese & Sinigaglia, 2010; Tsakiris et al., 2006). Intentional changes in the environment (e.g., lifting a cup) can only be caused by motor control over body parts (moving the hand towards the cup, grabbing it, etc.). This can be illustrated by the phrase 'I can affect the world by means of this body'. These two aspects (tactile sensation

and motor control) contribute to the perception of a strong connection between the own body and the phenomenal self, and ultimately to the development of a bodily self (Rochat, 1998).

Both the sense of ownership and the sense of agency can be manipulated within the paradigm of the rubber hand illusion (RHI), which is based on the multisensory integration of conflicting information about body posture (Botvinick & Cohen, 1998; Kalckert & Ehrsson, 2012, 2014; Kammers, Longo, et al., 2009; Tsakiris, Longo, & Haggard, 2010; Tsakiris et al., 2006). In the RHI, an artificial hand is placed visibly in front of the participant, whose own hand is hidden from view. By synchronously touching the artificial and the real hand, or by synchronizing the movements of both hands, a multisensory conflict between visual and proprioceptive information about hand posture can be induced, resulting in the illusory feeling of ownership and/or agency over the artificial hand (Kammers, Longo, et al., 2009; Riemer, Kleinböhl, Hölzl, & Trojan, 2013; Tsakiris, Longo, et al., 2010; Tsakiris et al., 2006). The subjective feeling of embodiment is accompanied by a shift of the perceived location of the own hand towards the artificial hand, a phenomenon generally referred to as proprioceptive drift (Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Tsakiris et al., 2006).

Many studies indicate that the embodiment of artificial hands depends on an anatomically plausible appearance (Haans, Ijsselstein,

* Corresponding author at: Aging & Cognition Research Group, German Center for Neurodegenerative Diseases (DZNE), Leipziger Str. 44, 39120 Magdeburg, Germany. Tel.: +49 391 67 24582; fax: +49 391 67 24528.

E-mail address: martin.riemer@dzne.de (M. Riemer).

& de Kort, 2008; Holmes, Snijders, & Spence, 2006; Tsakiris, Carpenter, James, & Fotopoulou, 2010) and the perceived connectedness to the body (Ehrsson, Spence, & Passingham, 2004; Pavani, Spence, & Driver, 2000), revealing some limitations regarding the plasticity of body representations (Tsakiris & Haggard, 2005). On the other hand, remarkable changes in body representations have been reported after visual exposure to anatomically implausible (e.g., an lengthened arm, Armel & Ramachandran, 2003; Kilteni, Normand, Sanchez-Vives, & Slater, 2012; Preston & Newport, 2012; Schaefer, Flor, Heinze, & Rotte, 2007) and even after anatomically impossible body configurations (e.g., a third arm, Schaefer, Heinze, & Rotte, 2009; Guterstam, Petkova, & Ehrsson, 2011, but see Folegatti, Farne, Salemme, & de Vignemont, 2012).

In a study by Schaefer, Noennig, Heinze, and Rotte (2006), participants received tactile stimuli at the little finger of their left hand while watching synchronous stimulations on the thumb of a virtual hand. Participants reported a referred sensation (i.e., they felt the touches on their thumb instead of their little finger), the degree of which was significantly correlated with short-term alterations in the topography of the primary somatosensory cortex. This raises the question whether alterations of body representations depend more on the consistency of visual feedback than on its congruence with somatosensory stimuli, because in the study by Schaefer et al. (2006) the somatosensory effects of the visible stimuli were absolutely stable and predictable. In other words, the mapping between real and artificial body parts was incongruent in a very consistent manner.

In a similar study by Kammers, Longo, et al. (2009, experiment 2), participants received tactile stimuli at their own index and little finger and viewed temporally synchronous stimuli at an artificial hand, either at congruent or incongruent positions. The mapping between real and artificial fingers was consistent within each experimental condition, and thus the perceived sensations were predictable from the viewed stimulation. Kammers, Longo, et al. (2009) reported enhanced subjective embodiment and proprioceptive drift after congruent as compared to incongruent stimulation. This result shows that a congruent mapping is an important factor within the RHI, but it does not provide insights into the impact of the predictability of tactile sensations, because this factor was kept constant and the effects of incongruent touch were not compared to an asynchronous or unpredictable condition. In other words, incongruent (but consistent) mapping between real and artificial fingers diminishes the RHI when compared to congruent mapping, but it might still affect body representations relative to temporally asynchronous stimulation, which is the conventional reference for measuring RHI effects. In a recent study, Ferri, Chiarelli, Merla, Gallesse, and Costantini (2013) reported that mere expectation of touch is sufficient to induce a sense of ownership over an artificial hand.

Especially for the emergence of a sense of agency, the predictability of body movements is an important factor, even if movements are discordant with efferent motor commands (Sato, 2009; Synofzik, Thier, & Lindner, 2006; Wegner, Sparrow, & Winerman, 2004; Wegner & Wheatley, 1999). In the study by Wegner et al. (2004), participants experienced control over other person's movements, only when those movements were reliably announced. Therefore, a consistent and predictable mapping between motor commands and body movements might partly compensate for their incongruence. Several studies suggest a specific role of motor activity for modulations of body representations (Braun et al., 2001; Schaefer, Flor, Heinze, & Rotte, 2005), and distorted visual feedback regarding own hand movements reduces the sense of agency (Farrer & Frith, 2002; Farrer, Bouchereau, Jeannerod, & Franck, 2008). Other studies investigated the effect of a congruent mapping between executed and observed movements (Fink et al., 1999; Foell, Bekrater-Bodmann, McCabe, & Flor, 2013), and there is evidence that humans are extremely sensitive to incongruent visual feedback about their own movements at a very early developmental stage (Morgan & Rochat, 1997).

There is another reason to assume a different impact of predictability when it comes to active movements as compared to passive touch. Regarding motor control, predictability refers to the phenomenal self as cause of effects produced in the environment, whereas in tactile sensation it refers to the environment as cause of effects imposed on the phenomenal self. It seems plausible that the prediction of produced effects (i.e., body movements) is more important than the prediction of induced effects (i.e., tactile sensations), because the former can be actively controlled while one is passively exposed to the latter.

The aim of the present study was twofold. First, we investigated the impact of congruent vs. incongruent mappings between touches or movements at real and artificial fingers on changes in body representations. Second, we examined the role of predictability regarding tactile sensations and body movements. We implemented a tactile and a motor version of the RHI paradigm, based on passive tactile stimulation or active voluntary movements of the artificial and the real hand, respectively. Incongruence was realized by an anatomically reversed mapping of index and middle fingers between the artificial and the real hand. Such an incongruent mapping between real and artificial fingers is, when consistently applied, nevertheless predictable, so predictability was manipulated by a random variation of congruent and incongruent mappings.

Embodiment of the artificial hand was quantified by phenomenal self-reports (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008) and a perceptual measure of proprioceptive drift (Riemer et al., 2013).

2. Methods

2.1. Participants

28 right-handed participants (7 males, mean age was 27.8 years) were recruited from the University of Mannheim and the local community. Participation was compensated either monetarily or with course credits (for psychology students). All participants gave written informed consent to the experiment.

2.2. Experimental set-up

Participants sat at a desk and placed their hands in a wooden framework (125 cm * 50 cm * 25 cm), as depicted in Fig. 1a. They watched an artificial wooden hand containing flexible joints at the sockets of the digits, placed 15 cm to the left of their own right hand, which was hidden from view by an occluding screen. Distances between artificial and real hands are measured from the index fingers. To provide a more realistic appearance, a skin-colored rubber glove was slipped over the artificial hand. Participants were instructed to adjust their body midline halfway between the artificial right hand and their own left hand, which was placed 31 cm to the left of the artificial hand. Index and middle fingers of the artificial hand could be lifted and lowered via pneumatically driven plungers, which were embedded in the framework and controlled by capacitive sensors placed beneath the participants' right index and middle fingers. In this vein, the experimental set-up enabled the experience of control over the finger movements of the artificial hand (Riemer et al., 2013).

2.3. Experimental conditions

For both the tactile and the motor induction methods, four experimental conditions were implemented (Table 1).

In the congruent condition, the participants' right hand and the artificial hand were stroked synchronously with two paint brushes in a congruent manner (i.e., either both index fingers or both middle fingers). The incongruent condition consisted in synchronous stroking of unrelated fingers (i.e., the real index and the artificial middle finger or the real middle and the artificial index finger). Importantly, in both the congruent and the incongruent condition the mapping between

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