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Higher-order cognitive factors affect subjective but not proprioceptive aspects of self-representation in the rubber hand illusion

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ABSTRACT

In the current study we look at whether subjective and proprioceptive aspects of self-representation are separable components subserved by distinct systems of multisensory integration. We used the rubber hand illusion (RHI) to draw the location of the 'self' away from the body, towards extracorporeal space (Out Condition), thereby violating top-down information about the body location. This was compared with the traditional RHI which drew position of the 'self' towards the body (In Condition). We were successfully able to draw proprioceptive position of the limbs in and out from the body suggesting body perception is a purely bottom-up process, resistant to top-down effects. Conversely, we found subjective self-representation was altered by the violation of top-down body information – as the strong association of subjective and proprioceptive factors found in the In Condition became non-significant in the Out Condition. Interestingly, we also found evidence that subjective embodiment can modulate tactile perception.

1. Introduction

Processes of multisensory integration underlie the most fundamental aspects of self-representation (Blanke, 2012; Blanke & Metzinger, 2009; Jeannerod, 2006). Indeed, it has been proposed that human bodily self-consciousness at its most basic, pre-reflexive level results from the constant presence and integration of information from our multiple sensory systems (Gallagher, 2005; Tsakiris, 2010). Bodily self-representation, however, is not as stable as it appears to the individual. Experimental perceptual illusions that disrupt body representation by manipulating multisensory inputs provide compelling evidence that, despite its perceived constancy, our representation of self can be easily and profoundly modified (Armel & Ramachandran, 2003; Botvinick & Cohen, 1998; Ehrsson, 2007; Ehrsson, Spence, & Passingham, 2004; Lenggenhager, Tadi, Metzinger, & Blanke, 2007). These findings highlight one of the most important topics in psychology and neuroscience today, the extent of human neural plasticity in immediate response to experience.

1.1. Experimental manipulation of self-representation: The rubber hand illusion

The rubber hand illusion (RHI) is a widely employed paradigm that demonstrates how perception of the body can be manipulated through the presentation of incongruous visual and tactile inputs administered to the hands (Botvinick &

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Cohen, 1998). Typically, in this illusion a participant's hand is concealed from view and replaced with a rubber prosthesis. The prosthesis is placed in the approximate position and angle of the participant's concealed limb, while introducing a slight spatial deviation between the two (with the rubber hand closer in towards the body midline than the real hand). The participant's own hand and the rubber hand then receive identical tactile stimulation (RHI induction), usually in the form of stroking with a paintbrush – precisely synchronising the timing and location of strokes. This creates a match between what is seen on the rubber hand and what is felt on the participant's hidden hand.

During the RHI, there are a number of effects on self-representation. These effects can be divided into the general categories of **subjective** (Botvinick & Cohen, 1998; Costantini & Haggard, 2007; Ehrsson, Holmes, & Passingham, 2005; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007), **proprioceptive** (Botvinick & Cohen, 1998; Holle, McLatchie, Maurer, & Ward, 2011; Rohde, Di Luca, & Ernst, 2011) and **physiological** outcomes (Barnsley et al., 2011; Moseley et al., 2008).

The subjective effects of the illusion refer to general alterations in the psychological, bodily experience of an individual, i.e. changes in how their body and their body parts *feel*. These subjective outcomes are thought to reflect the experience of incorporating the rubber hand into the participant's own body representation as well as rejection of their actual hand (Botvinick & Cohen, 1998; Ehrsson et al., 2004; Tsakiris, 2010). These outcomes are generally assessed using a questionnaire or verbal report.

The RHI also produces changes in the perceived location of the participant's hand, shifting it from its actual location towards the location of the rubber hand. There are a number of methods for assessing this proprioceptive change. Typically, participants are asked to estimate the position of their hidden hand before and after RHI induction and the systematic error caused by the illusion is measured. This can be achieved through verbal report of the perceived location or pointing with the unstimulated hand (i.e. behavioural measures). This change is often referred to as proprioceptive *drift*.

Various physiological changes have been identified following RHI, including alterations in temperature (Moseley et al., 2008), immune function (Barnsley et al., 2011) and galvanic skin response (Armel & Ramachandran, 2003) in the stimulated hand compared to the control hand. These changes are thought to reflect the disruption of subjective ownership of that limb (Barnsley et al., 2011; Moseley et al., 2008).

1.2. New evidence suggests original models of RHI mechanisms are incorrect

In the popular model put forward by Tsakiris (2010), induction of the RHI produces changes in subjective self-representation which, in turn, produce the alterations in proprioception. In this conceptualisation, subjective outcomes **cause** proprioceptive outcomes and therefore are considered a *behavioural proxy*.

Contrary to this model, new behavioural evidence suggests that subjective and proprioceptive RHI outcomes are in fact dissociable. For example, a number of studies have demonstrated proprioceptive drift towards a rubber hand without associated increases in felt ownership over the rubber hand, when the participant's hand is kept still (Holle et al., 2011; Rohde et al., 2011) and when making point-to-target actions (Holmes, Snijders, & Spence, 2006).

Longo, Schüür, Kammers, Tsakiris, and Haggard (2008) conducted a large-scale qualitative analysis of first-person RHI experience. They found Location (representing proprioceptive change) and Ownership scales to be significant independent predictors of proprioceptive change levels, indicating that perceived limb shifts should be considered separately from subjective ownership of the rubber hand.

Subjective and proprioceptive aspects of self-representation are also shown to be distinct in their relationship with other aspects of perception (Longo et al., 2008). Longo et al. (2008) investigated the relationship of RHI outcomes to participant's ratings of similarity in appearance between their hand and the rubber hand. Individuals who reported high levels of subjective illusion intensity on a questionnaire reported significantly greater similarity in appearance than those who experienced low subjective levels of illusion. Notably, when comparing objective measures of similarity (made by a double-blind observer), there were no actual appearance differences between the high and low subjective illusion groups. Given the objective similarity in appearance, and that the similarity judgements were collected *following* illusion induction, the authors concluded the effectiveness of the ownership manipulation caused the rubber hand to be perceived as more similar to the participant's own hand – rather than the other way around. There was no such relationship with proprioceptive indicators of the illusion indicating shifting limb-location did not change visual perception of the rubber hand in the same way.

Neurophysiological evidence also indicates the existence of separate components of body representation that are subserved by distinct neural systems. Kammers et al. (2008) administered rTMS over the inferior posterior parietal lobe (IPL) during RHI induction. They found significant reductions in immediate proprioceptive judgements of limb position while subjective ownership over the rubber hand and ballistic action responses were unaffected.

1.3. Multimodal models of self-representation

It now appears self-representation is not supported by one homogenous neurocognitive system, and that distinct systems support proprioceptive position estimation and higher-order subjective body-representations (Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Kammers et al., 2008; Rohde et al., 2011). While the tight integration of all self-representation systems is critical to the production of a coherent, global 'sense of self', it appears these subsystems may be driven by very different processes of multisensory integration at disparate neural locations.