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The rubber hand illusion in action

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ABSTRACT

In the well-known rubber hand illusion (RHI), watching a rubber hand being stroked while one's own unseen hand is synchronously stroked, induces a relocation of the sensed position of one's own hand towards the rubber hand [Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. *Nature, 391*(6669), 756]. As one has lost the veridical location of one's hand, one should not be able to correctly guide one's hand movements. An accurate representation of the location of body parts is indeed a necessary pre-requisite for any correct motor command [Graziano, M. S. A., & Botvinick, M. M. (1999). How the brain represents the body: Insights from neurophysiology and psychology. In D. Gopher, & A. Koriat (Eds.), *Attention and performance XVII—Cognitive regulation of performance interaction of theory and application* (pp. 136–157)]. However, it has not yet been investigated whether action is indeed affected by the proprioceptive drift towards the rubber hand, nor has the resistance of visual capture in the RHI to new proprioceptive information been assessed. In the present two kinematic experiments, we show for the first time that action resists the RHI and that the RHI resists action. In other words, we show a dissociation between illusion-insensitive ballistic motor responses and illusion-sensitive perceptual bodily judgments. Moreover, the stimulated hand was judged closer to the rubber hand for the perceptual responses, even after active movements. This challenges the view that any proprioceptive update through active movement of the stimulated hand erases the illusion. These results expand the knowledge about representations of the body in the healthy brain, and are in line with the currently most used dissociation between two types of body representations so far mainly based on neuropsychological patients [Paillard, J. (1991). Knowing where and knowing how to get there. In J. Paillard (Ed.), *Brain and space* (pp. 461–481); Paillard, J. (1999). Body schema and body image: A double dissociation in deafferented patients. In G. N. Gantchev, S. Mori, & J.Massion (Eds.), *Motor control, today and tomorrow* (pp. 197–214)].

1. Introduction

The way we use sensory information determines the way we encode it. Separate visual cortical processing pathways for perception and action are an illustration of this general principle (Milner & Goodale, 1995). On the one hand, there are mental representations dedicated to the recognition and identification of the input. On the other hand, there are representations used to plan and control actions performed towards the input. This distinction is founded on an impressive amount of evidence from physiology, psychophysics, neuropsychology and neuroscience (Jacob & Jeannerod, 2003). It has been shown not only for vision, but also for the auditory modality (Belin & Zatorre, 2000), and more recently for proprioception and touch (Dijkerman & de Haan, 2007). Moreover, not only the representation of the external world varies depending upon its functional role, but also the representation of one's own body in the brain seems to depend on the task.

At present there is an ongoing debate about the existence of dissociable body representations (de Vignemont, 2007; Gallagher, 2005; Paillard, 1991 (chap. 24), 1999; Schwoebel & Coslett, 2005; Sirigu, Grafman, Bressler, & Sunderland, 1991). Influenced by the Perception-Action model, Paillard (1991, 1999), suggested a distinction between 'knowing where' and 'knowing how to get there', that is between the body image for perception (i.e. judgment of one's own bodily properties) and the body schema for action (i.e. information about the body necessary to move such as posture, limb size, and strength). The evidence provided to support this distinction relies mainly on neuropsychological dissociations

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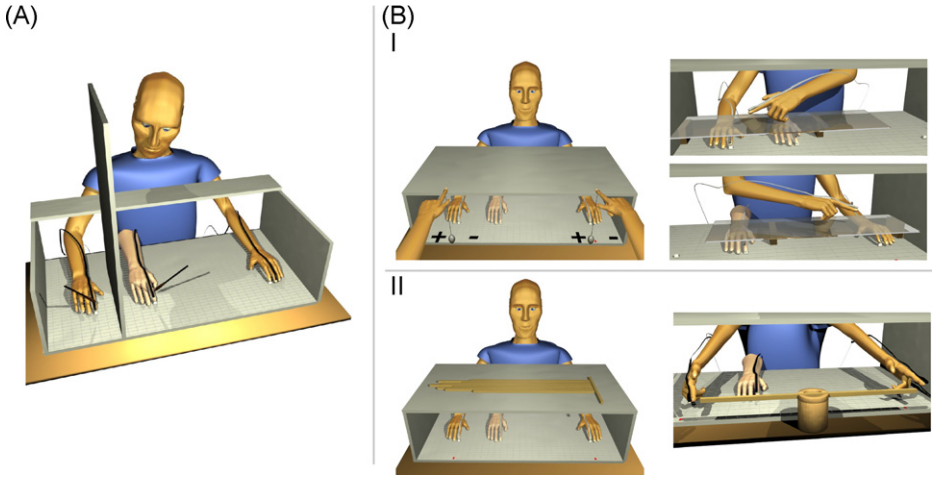

Fig. 1. Experimental set-up. (A) Set-up during stimulation period. (B) Perceptual and motor responses for Experiment 1 (I), and Experiment 2 (II).

between deafferentation and apraxia (disruption of body schema) (Buxbaum & Coslett, 2001), versus numbsense, neglect, and autotopagnosia (disruption of body image) (Gallagher, 2005; Head and Holmes, 1911–1912; Sirigu et al., 1991). However, there is almost a complete lack of evidence of a dissociation between different types of body representations in healthy individuals. One way of investigating these different body representations is through task-dependent effects of bodily illusions (Kammers, van der Ham, & Dijkerman, 2006). The rationale behind this is that the way the brain resolves the sensory conflict induced by the bodily illusion is a measurement of the plasticity and flexibility of the underlying body representation. Moreover, if the brain resolves this conflict differently depending on the type of task, this is taken as evidence that distinct body representations underlie these dissociable bodily experiences.

A well-known bodily illusion is the rubber hand illusion (RHI) (Botvinick & Cohen, 1998). In the RHI, participants see a rubber hand that lies in an anatomically congruent orientation to their own occluded hand. The rubber hand as well as the participant's own hand are stroked synchronously, creating the multisensory conflict of seeing a touch that is felt at a different location. This multisensory conflict is resolved by incorporation of the rubber hand in one's own body representation, as well as by relocation of the felt position of one's own hand towards the rubber hand. The general idea is that the illusion is based on visual capture of proprioceptive information. Proprioception drifts rapidly in the absence of vision, and in the RHI set-up this results in overwriting the proprioceptive location information of one's own hand with the visual location information of the rubber hand. On average 80% of participants report the RHI within 15 s of synchronous stroking (Ehrsson, Holmes, & Passingham, 2005; Lloyd, 2007).

Although synchrony between visual and proprioceptive information is necessary for the RHI to occur, this has proven not to be sufficient. The effect of the illusion is reduced or even eliminated when the posture or laterality of the rubber hand is incongruent with the unseen real hand (Armel & Ramachandran, 2003; Tsakiris & Haggard, 2005). This has led to the suggestion that prior representations about the body also play an important role (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005). If this is indeed the case, the extent of the RHI should depend on the type of body representation that is recruited by the response.

So far the RHI has been assessed mainly through questionnaires – to investigate the sense of ownership over the rubber hand, and perceptual judgments – to measure proprioceptive drift (Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007; Ehrsson et al., 2005; Ehrsson, Spence, & Passingham, 2004; Farne, Pavani, Meneghello, & Ladavas, 2000; Lloyd, 2007). The possible existence of multiple body representations has however been neglected, although it may differently influence the illusion depending on the type of task (de Vignemont, 2007; Gallagher, 2005; Paillard, 1999; Schwoebel & Coslett, 2005; Sirigu et al., 1991). In parallel with the task dependency found for several visual illusions (Aglioti, DeSouza, & Goodale, 1995; Goodale & Milner, 1992; Haffenden & Goodale, 2000; Kroliczak, Heard, Goodale, & Gregory, 2006), and in line with the dissociation between the body image and the body schema, we expected perceptual judgments to be more susceptible to bodily illusions than actions.

In the present study we therefore asked participants to indicate the felt position of their unseen stimulated hand by providing both perceptual judgments and motor responses (please see Fig. 1 for an example of RHIset-up). We conducted two experiments which both involved different types of action and perceptual responses to investigate the generality of a possible RHI task-dependency effect. All perceptual judgments are hypothesized to be predominantly based on the body image, whereas actions are thought to be governed primarily by the body schema (Kammers et al., 2006). While numerous studies have demonstrated that perceptual judgments are affected by the RHI, it is unknown whether this is true for motor responses. Botvinick and Cohen (1998) asked participants to point to the felt location of the occluded stimulated hand and found an endpoint bias towards the rubber hand. However, non-ballistic pointing movements display specific properties that differ from other types of actions (Kroliczak et al., 2006). Here we measured the kinematics of ballistic motor responses and investigated the effect these actions have on subsequent perceptual location judgments. The latter is of interest for two reasons. First, the general idea is that the RHI can arise because of drifting proprioceptive signals, active movements provide an update of this proprioceptive information, which is presumed to cancel out the RHI. However, this has not been tested. Second, if the motor and perceptual responses are indeed based on dissociable body representations, an effect of a preceding motor response on a subsequent perceptual judgment would shed light on the possible interaction between the two body representations.

2. Methods

2.1. Participants

Fourteen naïve right-handed participants (mean age = 22.9 years, S.D. = 4.01) gave informed consent and participated in Experiment 1. Another fourteen par-