**Title:** Is this my hand? Body-ownership and the rubber hand illusion

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**Abstract** We perceive that our body belongs to us and is a coherent and unified entity. Therefore, body-ownership is fundamental to self-consciousness. To explore body-ownership in normal subjects, researchers have intensively used a bodily illusion known as the rubber hand illusion (RHI). This review article focuses on RHI studies. In a standard RHI paradigm, the sight of the participant’s hand is occluded, while a life-sized fake hand is visible. Synchronous stroking of the fake and real hands with paintbrushes elicits a subjective sensation that the fake hand is their own. The RHI is generally demonstrated using a self-report questionnaire as a subjective measurement, and proprioceptive drift (i.e., mislocalization of the real hand toward the fake hand) as an objective measurement. There are two constraints for inducing the RHI: visuo-tactile synchrony and consistency between multisensory inputs and body representations. The RHI can also be induced by visuo-motor correlations: viewing movements of the rubber hand that are synchronous with movements of the real hand. In this RHI variant, participants experience body-ownership as well as agency, which is a type of bodily self-consciousness that one is initiating and controlling his/her own actions. Neuroimaging studies suggest that the RHI is associated with a wide range of neural substrates, including fronto-parietal networks. In sum, accumulating evidence from the RHI suggests that body-ownership is very flexible, and the brain can incorporate a non-corporal object into a person’s own body.

**Keywords:** bodily self-consciousness, multisensory integration, body representation, agency

**Introduction**

In daily life, we never mistake nearby objects or other people’s bodies as our own body. We consistently experience our body (parts) as belonging to us and as a coherent and unified entity separate from the external world. Therefore, body-ownership is fundamental to self-consciousness. Although we usually take it for granted, neuropsychological findings have shown abnormal body-ownership after impairments of the central and peripheral nervous systems. For example, right-hemisphere brain damage can induce somatoparaphrenic delusion whereby patients deny ownership of their body parts. Moreover, amputees frequently experience phantom sensations that their lost hands or legs still exist and belong to their body (called “phantom limb”). In rare cases, post-stroke patients perceive body-ownership of an additional limb (called “supernumerary phantom limb”). These phenomena suggest that body-ownership may be linked to specific cognitive processes or body representations. As a robust tool for examining body-ownership in healthy subjects, researchers have intensively used a bodily illusion known as the “rubber hand illusion” (RHI), which was first discovered by Botvinick and Cohen. In contrast to our intuition, accumulating evidence from the RHI has suggested that body-ownership is very flexible, and we can attribute a non-corporal object to our own body. This short review article focuses on RHI studies, especially on the following points. First, we introduce the RHI and how the strength of the RHI can be measured. Second, we note two distinct constraints for inducing the RHI in order to understand the cognitive processes involved. Third, we describe the relationships between body-ownership and agency in the RHI. Finally, we briefly review some neuroimaging studies of the RHI.
plicit measurement, self-reports of subjective feelings are assessed using a questionnaire with a 7-point Likert Scale ranging from +3 (agree strongly) to -3 (disagree strongly). In the original study by Botvinick and Cohen5), the RHI was related to the following items: “It seemed as if I were feeling the touch of the paintbrush in the location where I saw the rubber hand touched” and “I felt as if the rubber hand were my hand”. This approach is still used with minor modifications. In contrast, as an objective and implicit measurement, participants are required to judge the location of the real hand. The proprioceptive location shifts toward the rubber hand after the synchronous stroking (called “proprioceptive drift”). This technique is frequently used because moderate correlations have been observed between magnitude of drift and strength of the illusion5). However, recent findings have suggested that the two processes are distinct6,7). In other studies, the RHI was evaluated using the skin conductance response (SCR), which is a type of autonomic response. If the real hand is under risk of harm, humans experience a cold sweat, which can be evaluated using the SCR. Similarly, when the RHI is induced, if a knife or needle approaches the rubber hand8), or a fake finger is bent into a painful position9), the SCR is observed.

Bottom-up and top-down constraints for RHI induction

There are two constraints for inducing body-ownership of the rubber hand. One constraint is visuo-tactile synchrony. If visual and tactile stimulations are delivered asynchronously, the illusion is reduced or abolished. RHI induction requires a temporal discrepancy of less than 300 ms10,11). This bottom-up constraint indicates that multisensory integration between vision, touch, and proprioception is necessary for the RHI, based on a body map. First, watching the rubber hand being touched would induce an illusory tactile sensation on the unseen real hand, because vision is the predominant sense for localizing physical events in space12). Next, this visual capture of touch results in the mislocalization of the real hand toward the rubber hand (i.e., recalibration of the hand position), and consequently body-ownership of the rubber hand takes place.

Converging evidence has revealed that multisensory integration is necessary, but not sufficient, for the RHI. The other factor that influences the RHI is consistency between the inputs and preexisting body representations, which is a top-down constraint. For example, when a non-body-part object (wooden stick) or an anatomically-implausible rubber hand (i.e., contralateral hand) is used, the RHI cannot be induced13). Furthermore, when the rubber hand is rotated by 90 or 180 degrees (i.e., incongruent anatomical posture) with respect to the real one, the RHI is abolished13,14). If the rubber hand is systematically rotated, the subjects experience greater body-ownership when the angles are easier to imitate with the real hand15). In addition, the spatial distance between the rubber and the real hand modulate the RHI. For example, Lloyd16) found that the strength of the RHI is greatest when the distance is smallest, and decreases significantly beyond 27.5 cm. The author inferred that the boundary (c. 30 cm) for RHI induction results from the response property of bimodal neurons representing peripersonal space17), which have been found in the premotor and posterior parietal cortices of monkeys and respond to tactile stimulation of the hand and vision of objects surrounding the hand18). A more recent study showed that the distance between the rubber hand and the body midline also affects RHI induction19), indicating that peripersonal space centered both on the hand and the trunk may modulate the illusion.

Relationships between body-ownership and agency in RHI

The RHI can be induced not only by synchronous visuo-tactile stimulation, but also visuo-motor correlations: viewing movements of the rubber hand that are synchronous with movements of the real hand20-26). In this variant of the RHI, participants experience body-ownership as well as agency, which is a type of bodily self-consciousness of initiating and controlling our own actions. However, there is a difference from that induced by classic RHI. Tsakiris, Prabhu, and Haggard20) examined proprioceptive drift in the two methods, in which subjects watched a projected image of their hand. When a finger was stroked with a paintbrush or moved passively, proprioceptive drift could be observed, but only in the finger that was stroked or moved19). Conversely, if the finger was moved actively, the drift spread to other fingers. The authors suggest that mere afferent processes induce the
RHI, but in a fragmented manner, whereas efferent processes (i.e., agency) integrate body parts into a coherent and unified bodily consciousness\(^{77}\). Moreover, Kalckerkert and Ehrsson\(^{41}\) showed evidence for a double dissociation of body-ownership and agency using a rubber hand whose finger could be controlled by moving the subject’s index finger. The movements were controlled by the subject (active) or experimenter (passive), and the rubber hand was placed in an anatomically congruent or incongruent position. Self-reports revealed that passive movements could induce body-ownership, but not agency, while the incongruent position of the rubber hand abolished body-ownership, but left agency intact. However, the double dissociation was incomplete because agency was greater when the rubber hand’s position was anatomically congruent. Similar interactions between body-ownership and agency were reported in more recent studies\(^{28,29}\).

**Neural correlates underlying the RHI**

Using functional magnetic resonance imaging, several studies have examined the neural mechanisms underlying body-ownership over the rubber hand. Ehrsson, Spence, and Passingham\(^{14}\) found that activity in the bilateral ventral premotor cortices, cerebellum, and intraparietal cortex was associated with the RHI. Especially, the strength of the illusion measured through questionnaire ratings correlated with the magnitude of ventral premotor activity. As noted above, the premotor and parietal cortices have multimodal neurons. Multimodal integration in the premotor cortex may reflect body-ownership, whereas that in the parietal cortex may be associated with recalibration of the hand position\(^{30}\). Ehrsson et al.\(^{31}\) also reported that a threat to the rubber hand could induce activity in the anterior insula and anterior cingulate cortex, which are related to anxiety and whose activity levels were the same as when the real hand was threatened. In addition, activity in these anxiety-related areas significantly correlated with that of the ventral premotor and intraparietal cortices. Moreover, a positron emission tomography study by Tsakiris et al.\(^{32}\) reported that the strength of the RHI measured by proprioceptive drift positively correlated with right frontal operculum and right posterior insula activity. In sum, neuroimaging studies suggest that body-ownership over the rubber hand is associated with a wide range of neural substrates, including the fronto-parietal networks.

**Conclusions**

Discovery of the RHI gave researchers a scientific approach for exploring bodily self-consciousness, especially body-ownership. The RHI indicates that our body-ownership is very flexible, and our brain can incorporate a non-corporeal object into our own body, although the precise underlying neural mechanism is still unknown. Behavioral evidence suggests that the RHI results from multisensory integration (bottom-up processes) and interactions between multisensory inputs and body representations (top-down processes). Knowledge of body-ownership could influence rehabilitation (e.g., prosthetic limb), engineering (e.g., virtual reality techniques; VR), and brain machine interfaces (BMI). Future studies should explore interactions between body-ownership and agency under VR and BMI, long-term modulation of body-ownership in rehabilitation, and neural networks underlying body-ownership in cognitive neuroscience.

**Conflict of Interests**

The authors declare that there is no conflict of interests regarding the publication of this article.

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