1. Experimenting with body-ownership

At the inaugural lecture of the Centre for Subjectivity Research (Copenhagen, Denmark), Waldenfels referred to the riddle of “how to justify the fact that a certain physical body is called my own body (corpus meum) and how to find out whether there are other bodies that are animated by other minds” (Waldenfels, 2004, p. 235). In essence, the riddle mentioned by Waldenfels refers to the foundations of the experience of one’s own body: “What grounds my experience of my body as my own? The body that one experiences is always one’s own, but it does not follow that one always experiences it as one’s own” (de Vignemont, 2007, p. 427). Empirical research on the bodily self has only recently started to investigate how the link between a body and the experience of this body as mine is developed, maintained or disturbed. The Rubber Hand Illusion has been used as a model instance of the normal sense of embodiment to investigate the processes that underpin the experience of body-ownership. This review puts forward a neurocognitive model according to which body-ownership arises as an interaction between current multisensory input and internal models of the body. First, a pre-existing stored model of the body distinguishes between objects that may or may not be part of one’s body. Second, on-line anatomical and postural representations of the body modulate the integration of multisensory information that leads to the recalibration of visual and tactile coordinate systems. Third, the resulting referral of tactile sensation will give rise to the subjective experience of body-ownership. These processes involve a neural network comprised of the right temporoparietal junction which tests the incorporeability of the external object, the secondary somatosensory cortex which maintains an on-line representation of the body, the posterior parietal and ventral premotor cortices which code for the recalibration of the hand-centred coordinate systems, and the right posterior insula which underpins the subjective experience of body-ownership. The experience of body-ownership may represent a critical component of self-specificity as evidenced by the different ways in which multisensory integration in interaction with internal models of the body can actually manipulate important physical and psychological aspects of the self.

My body in the brain: A neurocognitive model of body-ownership

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ABSTRACT

Empirical research on the bodily self has only recently started to investigate how the link between a body and the experience of this body as mine is developed, maintained or disturbed. The Rubber Hand Illusion has been used as a model instance of the normal sense of embodiment to investigate the processes that underpin the experience of body-ownership. This review puts forward a neurocognitive model according to which body-ownership arises as an interaction between current multisensory input and internal models of the body. First, a pre-existing stored model of the body distinguishes between objects that may or may not be part of one's body. Second, on-line anatomical and postural representations of the body modulate the integration of multisensory information that leads to the recalibration of visual and tactile coordinate systems. Third, the resulting referral of tactile sensation will give rise to the subjective experience of body-ownership. These processes involve a neural network comprised of the right temporoparietal junction which tests the incorporeability of the external object, the secondary somatosensory cortex which maintains an on-line representation of the body, the posterior parietal and ventral premotor cortices which code for the recalibration of the hand-centred coordinate systems, and the right posterior insula which underpins the subjective experience of body-ownership. The experience of body-ownership may represent a critical component of self-specificity as evidenced by the different ways in which multisensory integration in interaction with internal models of the body can actually manipulate important physical and psychological aspects of the self.

1. Experimenting with body-ownership

At the inaugural lecture of the Centre for Subjectivity Research (Copenhagen, Denmark), Waldenfels referred to the riddle of “how to justify the fact that a certain physical body is called my own body (corpus meum) and how to find out whether there are other bodies that are animated by other minds” (Waldenfels, 2004, p. 235). In essence, the riddle mentioned by Waldenfels refers to the foundations of the experience of one’s own body: “What grounds my experience of my body as my own? The body that one experiences is always one’s own, but it does not follow that one always experiences it as one’s own” (de Vignemont, 2007, p. 427). Empirical research on the bodily self has only recently started to investigate how the link between a body and the experience of this body as mine is developed, maintained or disturbed.

Motor cognition operationalizes the self as a physical entity underpinned by the processing of multisensory and motor signals that generate the experiences of ownership over her body and agency over her actions. Recent approaches stemming out from this emphasis on sensorimotor processing and its relevance for higher cognition have attempted to explain these two basic senses of one’s body: the sense of agency and the sense of body-ownership. The two senses of body-ownership and agency jointly constitute a minimal, bodily, sense of self, but their exact relation remains unknown. It is not in the purpose of this review to discuss the interactions between body-ownership and agency (for a discussion see Synofzik, Vosgerau, & Newen, 2008; Tsakiris, Schütz-Bosbach, & Gallagher, 2007). Instead, the focus will be on the sense of body-ownership per se. Body-ownership refers to the special perceptual status of one’s own body, which makes bodily sensations seem unique to oneself, that is, the feeling that “my body” belongs to me, and is ever present in my mental life (Gallagher, 2000).

William James noted that contrary to the perception of an object, which can be perceived from different perspectives or even cease to be perceived, we experience “the feeling of the same old body always there” (James, 1890/1981, p. 242). Echoing James, Merleau-Ponty (1962) wrote that “[…] the permanence of my own body is entirely different in kind … Its permanence is not a permanence in the world, but a permanence on my part” (p. 90). This seemingly inescapable permanence of the body raises interesting methodological problems in our attempt to study body-ownership scientifically. Classical experimental designs in psychology involve the direct comparison between conditions where the phenomenon under investigation is either present or absent. The experimental isolation of body-ownership by direct manipulations that make the body present in one experimental condition but absent in another.
would seem problematic, if not impossible. Early studies on the bodily self-focused mainly on self-recognition in human and non-human primates. Jeannerod and colleagues performed a series of experiments on self-recognition of bodily movements (for a review see Jeannerod, 2003). In most studies of self-recognition, participants see a body-part, which may or may not be related to their own body, and judge whether it is their own body-part or not. The information available to support this judgment is systematically varied across conditions, for example by moving the hand (Daprati et al., 1997; Sirigu, Daprati, Pradat-Diehl, Franck, & Jeannerod, 1999; Tsakiris, Haggard, Franck, Mainy, & Sirigu, 2005), by introducing delays between the movement and the visual feedback (Franck et al., 2001), or by rotating the hand image (Van den Bos & Jeannerod, 2002). Self-recognition requires the monitoring and integration of various sources of information such as intention, efferent and afferent signals in a short time-window. The tasks require an explicit self-recognition judgment: the participant's body-part is objectified, that is, a body-part is presented like an external object projected on a screen, and the experimental manipulations focus on the conditions under which this body-part will be judged as mine. Therefore, these experiments involve explicit judgments of agency (e.g. “was that your action?”) and body-ownership (e.g. “was that your hand?”), rather than the feeling of agency and body-ownership per se (see also Synofzik et al., 2008). Experimentation with the feeling of body-ownership becomes possible when one uses multisensory stimulation as a means of altering the experience of the body: the experience of body-ownership being present in one condition, and absent in another.

The Rubber Hand Illusion (RHI) emerged as an experimental paradigm that allows the controlled manipulation of the experience of body-ownership. In brief, watching a rubber hand being stroked synchronously with one's own unseen hand causes the rubber hand to be attributed to one's own body, to “feel like it's my hand” (Botvinick & Cohen, 1998). This illusion does not occur when the rubber hand is stroked asynchronously with respect to the subject's own hand. One behavioural correlate of the RHI is an induced change in the perceived location of the participant's own hand towards the rubber hand. Botvinick and Cohen (1998) showed that, after synchronous visuo-tactile stimulation of the rubber hand and the participant's hand, participants perceived the position of their hand to be closer to the rubber hand than it really was. Similar patterns of mislocalizations and proprioceptive drifts have been obtained with different response methods (see Tsakiris, 2007 for a review, and Kammers et al., 2008 for a dissociation between different response types). Interestingly, the prevalence of the illusion over time (Botvinick & Cohen, 1998) and the subjective intensity of the experience of body-ownership (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008) are positively correlated with changes in the felt location of the subject's own hand towards the rubber hand. The successful manipulation of body-ownership during the RHI has been demonstrated in several replication studies (Armel & Ramachandran, 2003; Ehrsson, Spence, & Passingham, 2004; Longo et al., 2008; Tsakiris & Haggard, 2005; Tsakiris, Hesse, Boy, Hagard, & Fenk, 2007; Tsakiris, Schütz-Bosbach et al., 2007) and modifications of the classic paradigm (Austen, Soto-Faraco, Enns, & Kingstone, 2004; Capelari, Uribe, & Brasil-Neto, 2009; Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007; Ehrsson, 2007; Ehrsson et al., 2008; Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007; Häggi et al., 2008; Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Kanayama, Sato, & Ohira, 2007; Kanayama, Sato, & Ohira, 2008; Lenggenhager, Tadi, Metzinger, & Blanke, 2007; Petkova & Ehrsson, 2008; Schütz-Bosbach, Mancini, Aglioti, & Haggard, 2006; Schütz-Bosbach, Avenanti, Aglioti, & Haggard, 2009; Schütz-Bosbach, Tausche, & Weiss, 2009; Slater, Perez-Marcos, Ehrsson, & Sanchez-Vives, 2008; Tsakiris, Prabhu, & Haggard, 2006) since the original study (Botvinick & Cohen, 1998).

The RHI paradigm is one of the few viable ways of investigating body-ownership scientifically because it allows for an external object to be treated, rather than simply recognized, as part of my body. The present review will argue that the experimental paradigm of the RHI can inform a viable model of the normal experience of body-ownership in general, in contrast to self-recognition and tool-use paradigms that tackle different cognitive processes, such as body-recognition and body-extension, respectively. The following sections will review the phenomenology of body-ownership (see Section 2), the roles of multisensory integration and of cognitive (i.e. non-primarily sensory) body-representations for body-ownership (see Sections 3 and 4). Sections 5 and 6 present a neurocognitive model of body-ownership in terms of information processing (Section 5) and its neural substrates (Section 6). The review concludes with recent extensions of the body-ownership studies to full bodies and self-identity.

2. What is the experience of body-ownership like?

A large sample study (Longo et al., 2008) investigated the subjective experience during the RHI by asking participants to complete a 27-item questionnaire after each of the synchronous and asynchronous blocks of visuo-tactile stimulation. A Principal Component Analysis (PCA) revealed that the subjective experience of ownership of the rubber hand consists of distinct dissociable components present in both synchronous and asynchronous conditions (Longo et al., 2008; ownership (e.g. rubber hand as part of one's body); location (i.e. the rubber hand and one's own hand were in the same place, also to sensations of causation between the seen and felt touches); and agency (i.e. being able to move the rubber hand and control over it). A further analysis focused on the relation between the component scores and the behavioural proxy of the RHI used in this study (i.e. proprioceptive drift obtained with the method described in Tsakiris & Haggard, 2005). Embodiment of rubber hand in general significantly predicted the proprioceptive displacement.

A follow-up study (Longo, Schüür, Kammers, Tsakiris, & Haggard, in 2009) used the same sample to investigate the extent to which the experience of ownership over the rubber hand may impact on the perceived similarity between the participant's own hand and the rubber hand. Objective similarity with regards to skin luminance, hand shape, and third-person similarity ratings did not appear to influence participants' experience of the RHI. Conversely, the experience of ownership of the rubber hand altered the physical similarity that participants perceived between their own hand and the rubber hand. Participants who experienced the RHI perceived their hand and the rubber hand as significantly more similar, than participants who did not experience the illusion, suggesting that ownership leads to perceived similarity, but perceived similarity does not lead to ownership.

These studies, among the first to provide an in-depth and quantified analysis of the subjective experience during the RHI, demonstrate that the model instance of embodiment during the RHI induces a complex yet structured experience of body-ownership with identifiable components. Overall, it seems that three main aspects of embodiment are successfully manipulated during RHI: the sense of ownership of the rubber hand, the perceived location of the participant's own hand, and the perceived similarity of appearance of body-parts. A fourth, and perhaps the most intriguing component that could be involved in RHI is a change in the experience of one's own body during this illusion of body-ownership. Will the experienced ownership over a new body-part subsequently alter the experience of my body? One possibility is that the rubber hand is simply added as a third supernumerary limb to one's body, without actually affecting the experience
of one’s own hand. Alternatively, the rubber hand may replace the participant’s own hand, and in turn, alter the experience of one’s hand. Consistent introspective and behavioural measures suggest that the rubber hand is not simply added as a third limb, but instead replaces the real hand, both in terms of phenomenal experience and physiological regulation. Participants denied that they felt as if they had three hands, while they accepted the statement that that they felt as if their own hand had disappeared, and that their own hand was in the location where the rubber hand was (Longo et al., 2008). Therefore, accounts of the subjective RHI experience suggest that incurred changes do not consist of an addition or extension of one’s body, but instead they cause incorporation and moreover replacement of one’s own hand.

A recent study by Moseley et al. (2008) provides direct evidence that the experience of ownership during RHI is also accompanied by significant changes in the homeostatic regulation of the real hand, beyond changes in the subjective experience of one’s body. In particular, skin temperature of the real hand decreased when participants experienced the RHI. Additionally, the magnitude of the decrease in skin temperature on the participant’s own hand was positively correlated with the vividness of the illusion. Importantly, this effect was absent in the mere presence of synchronous visual and tactile stimulation (see Experiment 5 in Moseley et al., 2008), but occurred only as a result of the experience of ownership. Thus, experienced ownership over a new body-part has direct consequences for real body-parts that occur once participants experience the RHI, and not simply as the direct result of multisensory integration. Therefore, cognitive processes that disrupt the awareness of our physical self may in turn disrupt the physiological regulation of the self (Moseley et al., 2008). The changes caused in the physiological regulation of the self as a result of the experience of body-ownership over and above multisensory integration suggest that processes other than multisensory integration may be involved in generating, maintaining or disrupting the awareness of the bodily self.

3. The bottom-up account of body-ownership: the role of intermodal matching

Why and how is the rubber hand experienced as part of one’s body? In brief, the RHI reflects the malleability of the representation of the body caused by multisensory processing. Multisensory processing aims at the integration of sensory signals and the resolution of potential conflicts to generate a coherent representation of the world and the body. The RHI reflects a three-way weighted interaction between vision, touch, and proprioception: vision of tactile stimulation on the rubber hand captures the tactile sensation on the participant’s own hand, and this visual capture results in a mislocalization of the felt location of one’s own hand (e.g. the experimenter bent one of the rubber fingers backwards), Skin Conductance Responses (SCRs) measured from the subject’s unstimulated hand were significantly higher compared to the control asynchronous condition (Armel & Ramachandran, 2003). Similar differences, albeit smaller in magnitude, between SCRs for synchronous and asynchronous conditions were found when participants observed a table, instead of a rubber hand, being stroked while tactile stimulation was delivered on the participant’s own hand.1 According to Armel and Ramachandran (2003), both the rubber hand and the table, and in principle any other object, can be experienced as part of one’s body, provided that strong visuo-tactile correlations are present. Therefore, the illusion that “the fake hand/table is my hand”, and more general the sense of body-ownership, is the result of a bottom-up mechanism, which associates synchronous visuo-tactile events: any object can become part of “me”, simply because strong statistical correlations between different sensory modalities are both necessary and sufficient conditions for body-ownership.

Indeed, the possibility that body-ownership arises in a bottom-up fashion, as an accumulative effect of frequent and recurring multisensory correlations during ontogeny cannot be excluded. Developmental studies suggest that intermodal matching is a prerequisite for self-identification (Rochat & Striano, 2000). At the same time, developmental studies also suggest that at least some body-representations seem to be innate, facilitating intermodal matching. For example, Morgan and Rochat (1997) showed that 3-month-old infants, with relatively little experience of seeing their legs, are sensitive to left-right reversal of their own legs shown on a screen and to differences in the relative movements and/or the featural characteristics of the legs (i.e. the relative bending of the legs at the knees and ankles), supporting the idea of innate representations of the anatomical and structural features of a normative body. The extent to which multisensory input is the sole drive of body-ownership or not is a controversial issue at the heart of the neurocognitive understanding of body-ownership in particular, and of body-representations more generally (Berlucchi & Aglioti, 1997; Carruthers, 2008; de Vignemont, Tsakiris, and Haggard, 2005; Dijkerman & de Haan, 2007; Graziano & Botvinik, 2001; Holmes & Spence, 2006; Sirigu, Graffman, Bressler, & Sunderland, 1991; Tsakiris & Fotopoulou, 2008).

An alternative or complimentary approach to this bottom-up view of body-ownership would consider the top-down role played by non-primarily sensory representations of the body in addition to the contribution of current multisensory input. It is still debated whether current multisensory experience is assimilated to a reference model of anatomical and structural representations of the body, possibly arising from prior experience and also innate body-representations that involve more than the mere registration of peripheral inputs, and in that sense, they can be called “cognitive”. As broadly defined by Graziano and Botvinik (2001), body-representations involve the interpretation of peripheral inputs in the context of a rich internal model of the body’s structure; body-related percepts are not simply correlated, but they are integrated against a set of background conditions that preserve the coherence of bodily experience. These background conditions would require different types of body-representations to modulate the integration of current multisensory input in a top-down manner.

1 SCRs for the synchronous visuo-tactile stimulation when looking at a table were of the same magnitude as SCRs for the asynchronous visuo-tactile stimulation when looking at a rubber hand (M = 0.24, whereas mean SCR for the synchronous visuo-tactile stimulation when looking at a rubber hand was 0.34). As Armel and Ramachandran (2003) note, the rubber hand condition was significantly more effective at inducing the illusion than the table when measured by intensity ratings (p < 0.001), and marginally so for SCRs (p = 0.05).
ner. On this latter view, intermodal matching may not be sufficient for the experience of body-ownership.

4. Top-down modulations: the evidence against the bottom-up account

4.1. On corporal and non-corporal objects

If body-ownership was driven by synchronous multisensory stimulation as a sufficient condition, then we would expect to induce a sense of body-ownership over objects that do not resemble body-parts. Accumulating evidence suggests that the RHI is not induced when the rubber hand is replaced by a neutral non-corporal object such as a wooden stick (i.e. coding of visual form representations of body-parts, Haans, Ijsselsteijn, & de Kort, 2008; Tsakiris, Costantini, & Haggard, 2008; Tsakiris & Haggard, 2005, see also Holmes, Sniiders, & Spence, 2006; see also Graziano, Cooke, & Taylor, 2000, but cf. Armel & Ramachandran, 2003). Instead the viewed object should match a visual representation of the tactually stimulated body-part for the synchronous visuo-tactile stimulation to elicit a sense of body-ownership. Following on the work of Graziano et al. (2000) on bimodal neurons in monkeys and Tsakiris and Haggard (2005) on RHI, Haans et al. (2008) revisited the hypothesis that any object can be self-attributed if strong statistical correlations between vision and touch are present. Haans et al. (2008) assessed the strength of the RHI in a factorial design where a viewed object that could have a hand shape or not, with a natural-skin texture or not, was stimulated in synchrony with the participant’s own hand. The results, contrary to what Armel and Ramachandran (2003) predicted, showed that a hand-shaped object induced a stronger RHI as measured with a questionnaire than a non-hand-shaped object (see also Tsakiris, Carpenter, & James, in press; Tsakiris & Haggard, 2005). In contrast, the main effect of texture was not significant, while the interaction of shape by texture was significant because natural-skin texture increased the RHI strength for a hand-shaped object, but not for a non-hand-shaped object. These findings further support the hypothesis that the experience of ownership is not induced when the viewed object does not resemble the human hand, even if the texture is hand-like.

4.2. Anatomical and postural constrains

The experience of body-ownership during the RHI is abolished when the rubber hand is placed in an incongruent anatomical posture with respect to one’s own hand (i.e. coding of postural representations of body-parts, see Costantini & Haggard, 2007; Tsakiris & Haggard, 2005, see also Graziano et al., 2000; Pavani, Spence, & Driver, 2000; but cf. Armel & Ramachandran, 2003), or when the rubber hand is of a different laterality with respect to one’s own stimulated hand (i.e. coding of anatomical representations of body-parts, see Tsakiris & Haggard, 2005).

Two elegant studies (Costantini & Haggard, 2007; Lloyd, 2007) have used parametric designs to investigate in greater detail the role of postural and spatial relations between the rubber hand and the participant’s own hand in inducing the RHI. Lloyd (2007) systematically varied the distance between the rubber hand and the participant’s own hand to quantify the spatial boundaries over which referred tactile sensations can be felt on a rubber hand. Introspective evidence showed that the strongest ratings of the illusion were collected when the distance between the two hands was closest (17.5 cm), while ratings of the RHI decayed significantly when the distance exceeded 30 cm. Lloyd (2007) suggests that these findings can be accounted by the receptive fields of bimodal visuo-tactile cells that encode peripersonal space around the subject’s own hand. When the rubber hand is in close proximity to the participant’s own hand (<27.5 cm), the visual representation of the rubber hand falls within the visual receptive field that surrounds the tactile receptive field of the participant’s own hand. This spatial proximity would be another necessary condition for body-ownership.

Costantini and Haggard (2007) investigated the effects of directional mismatch between the stimulation of the two hands, and equivalent mismatches between the postures of the two hands, either by adjusting stimulation or posture of the participant’s hand, or, by adjusting stimulation or posture of the rubber hand. The RHI survived small changes in the participant’s hand posture, but disappeared when the same posture transformations were applied to the rubber hand, while a mismatch between the direction of stimulation delivered to the participant’s hand and the rubber hand completely abolished the RHI as measured by proprioceptive drift. Interestingly, when the participant’s hand posture was slightly different from the rubber hand posture, the RHI remained as long as stimulation of the two hands was congruent in a hand-centred spatial reference frame, even though the altered posture of the participant’s hand meant that stimulation was incongruent in external space. Conversely, the RHI was reduced when the stimulation was incongruent in hand-centred space, but congruent in external space, suggesting that “a small transformation of what the subject sees reduces the illusion more than the equivalent transformation of what they feel” (Costantini & Haggard, 2007, p. 238). According to Costantini and Haggard (2007), first a transformation aligns the rubber hand with the subject’s own hand, and then the correlation between visual and tactile stimulation is computed.

Converging evidence from RHI studies (Costantini & Haggard, 2007; Ehrsson et al., 2004; Lloyd, 2007; Pavani et al., 2000; Tsakiris & Haggard, 2005), studies on visuo-tactile extinction on neuropsychological patients (di Pellegrino, Ladavas, & Farne, 1997; Farne, Dematte, & Ladavas, 2005; Ladavas, di Pellegrino, Farne, & Zeloni, 1998) and neurophysiological studies on monkeys (Graziano et al., 2000) suggests that correlated multisensory stimulation and spatial proximity are necessary but not sufficient for the integration of a visual stimulus to peripersonal space or for the experience of ownership during the RHI. Anatomical and postural correspondence between the visually stimulated body part and the tactually stimulated body-part are also necessary for body-ownership. These consistent findings suggest that factors other than the mere correlation between synchronized visual and tactile events modulate the experience of body-ownership.

5. Body-ownership as an interaction between current multisensory input and internal models of the body: a neurocognitive model of body-ownership

Makin, Holmes, and Ehrsson (2008) put forward a parsimonious account of the RHI based on processes of multisensory integration in peri-hand space (Maravita, Spence, & Driver, 2003), without the need of top-down modulation by body-representations. On their account, the RHI occurs when the following two conditions are met: first, the rubber hand should be situated in an anatomically plausible position, and second, the synchronous visual and tactile events should be both located near to the visible hand. Even though all the aforementioned modulations of the RHI take place within peripersonal space and exploit mechanisms of multisensory hand-centred representations of space (Lloyd, 2007; Makin et al., 2008), it seems unlikely that a full account of the experience of ownership during the RHI can be given solely on the basis of these mechanisms and their neural underpinnings. Note, that this account does not make any explicit predictions about the occurrence of RHI when the rubber hand is placed in an anatomically plausible position, but one that is incongruent to the participant’s own hand (see Costantini &
that occur after participants experience the RHI (see Moseley et al., 2008) and felt body-part (Graziano et al., 2000; Pavani et al., 2000; Tsakiris & Haggard, 2005), the volumetric congruency between the viewed and the felt body-part (Pavani & Zampini, 2007), the postural congruency between the viewed and the felt body-part (Austen et al., 2004; Costantini & Haggard, 2007; Ehrsson et al., 2004; Pavani et al., 2000; Tsakiris, Hesse et al., 2007; Tsakiris, Schütz-Bosbach et al., 2007). The third comparison is between the current sensory input, that is, between the vision of touch and the felt touch and their respective reference frames. The PPC underpins this third comparison by resolving the conflict between visual and tactile information and recalibrating the visual and tactile coordinate systems (Ehrsson et al., 2004; Makin et al., 2008). This recalibration will result in the touch referral, underpinned by activity in the premotor cortex (Ehrsson et al., 2004). Finally, the subjective experience of ownership, underpinned by activity in the right posterior insula (Tsakiris, Hesse et al., 2007; Tsakiris, Schütz-Bosbach et al., 2007), will update the body model, resulting in the incorporation of hand and subsequent physiological regulation of the body (Moseley et al., 2008). The crossed circle represents a comparator. The recycling arrow denotes a loop.

In addition, lesions in brain areas that underpin these processes such as the ventral premotor cortex and intraparietal sulcus (Makin et al., 2008) do not result in denial of body-ownership (Baier & Karnath, 2008). Makin et al. (2008) cite two studies by Arzy, Overney, Landis, and Blanke (2006) and Berti et al. (2005) to support the hypothesis that lesions in premotor cortex result in deficits in body-ownership. Arzy et al. (2006) report a case study of a patient who, following two small confined lesions in the right premotor and motor cortices, “felt that parts of her left arm had disappeared. Much to her surprise she could see the table on which she had rested her left arm as if she could see the table through the arm, and saw her left arm only above her elbow, with a clear-cut border” (p. 1022). The patient described by Arzy et al. (2006) displayed anosomatognosia (i.e. loss of awareness of one body-half (which may or may be not paralysed, see Critchley, 1953), but not somatoparaphrenia, that is, the patient did not report any experience of disownership (at least not as the case is reported). Similarly, the study by Berti et al. (2005) focused on patients with anosognosia for hemiplegia, a syndrome that is dissociable from somatoparaphrenia (Vallar & Ronchi, 2009). Finally, there are behavioural changes that occur after participants experience the RHI (see Moseley et al., 2008 and Section 2 above) that cannot be solely accounted by multisensory integration in peri-hand space, without considering other higher order representations of the body.

The aforementioned processes postulated by Makin et al. (2008) are indeed necessary for the experience of body-ownership. However, the studies reviewed in Section 4 converge on the hypothesis that multisensory integration in peripersonal hand space by itself is not sufficient for body-ownership. Instead, other factors such as the visual form congruency between the viewed object and the felt body-part (Haans et al., 2008; Tsakiris & Haggard, 2005; see also Holmes et al., 2006), the anatomical congruency between viewed and felt body-part (Graziano et al., 2000; Pavani et al., 2000; Tsakiris & Haggard, 2005), the volumetric congruency between the viewed and the felt body-part (Pavani & Zampini, 2007), the postural congruency between the viewed and felt body-part (Austen et al., 2004; Costantini & Haggard, 2007; Ehrsson et al., 2004; Pavani et al., 2000; Tsakiris & Haggard, 2005), and the spatial relation between viewed and felt body-part (Lloyd, 2007), modulate the induction of the RHI and the experience of body-ownership. Fig. 1 proposes a preliminary neurocognitive model of body-ownership that can account for the majority of the empirical findings to date and generate testable hypothesis for future research.

In the first critical comparison, the visual form of the viewed object is compared against a pre-existing body model that contains a reference description of the visual, anatomical and structural properties of the body (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005; Tsakiris, Costantini, & Haggard, 2008), that are
current postural configuration), as well as current reafferent information (as shown in the connection between touch and vision and body state in Fig. 1) will be informing this current state of the body. If there is incongruence between the posture of felt and seen hands, the seen hand will not be experienced as part of one’s own body, even if the multisensory stimulation between the two hands suggests otherwise (Costantini & Haggard, 2007; Ehrsson et al., 2004; Tsakiris & Haggard, 2005). The model predicts that discrepancies at the postural and anatomical level will reduce the experience of ownership. The third comparison is between current sensory input, that is, between the vision of touch and the felt touch and their reference frames. For large discrepancies in tactile and visual reference frames (Lloyd, 2007), the RHI will not occur. Similarly, temporal asynchrony between vision of touch and felt touch will not induce the subjective referral of touch to the rubber hand (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). The model predicts that discrepancies in the directional or temporal parameters of visuo-tactile stimulation will impede the recalibration of their reference frames and the subsequent touch referral, preventing, thus, the induction of the experience of ownership.

On the basis of the empirical findings reviewed above, body-ownership during the model instance of embodiment as studied in the RHI arises as an interaction between multisensory input and modulations exerted by stored and on-line internal models of the body (Tsakiris, 2007; Tsakiris & Haggard, 2005). This functional interaction between multisensory integration and body models should have identifiable neural signatures. Section 6 reviews a series of experiments investigating the distinct neural mechanisms that underpin the experience of body-ownership during the RHI. As described in the next section, the first critical comparison involves the contribution of a body-model underpinned by the right temporoparietal junction. The processes engaged in the second and third comparisons engage the anterior (i.e. SII, see Press et al., 2008; Tsakiris, Hesse et al., 2007; Tsakiris, Schütz-Bosbach et al., 2007) and posterior parietal cortices (Ehrsson et al., 2004; Kammers et al., 2008; Makin et al., 2008), with the premotor cortex underlying additional multisensory processes that produce the touch referral (Ehrsson et al., 2004). Finally, the subjective experience of body-ownership is underpinned by activity in the right posterior insula (Baier & Karnath, 2008; Tsakiris, Hesse et al., 2007).

6. A neural network for body-ownership

6.1. Testing for fit with the body-model: the contribution of rTPJ

How does the brain decide on the compatibility and eventual incorporeability of an external object? The behavioural (Tsakiris & Haggard, 2005) and electrophysiological (Press et al., 2008) data suggest that the process of filtering what may or may not become part of one’s body is not the same as the process of multisensory integration that drives the RHI. Tsakiris et al. (2008) suggested that current sensory stimuli are processed and finally tested-for-fit comparison 1).

Press et al. (2008) investigated whether the modulation of somatosensory processing by visuo-tactile processing is driven by bottom-up processes (i.e. temporal synchronicity of multisensory input) or by top-down processes (i.e. coherence with pre-existing body-representations). During training, participants viewed a rubber hand or a neutral object stimulated in synchrony or not, with stimulation of their own hand. During the test phase, somatosensory ERPs were recorded to tactile stimulation of the left or right hand, to assess how tactile processing was affected by previous visuo-tactile training. An enhanced somatosensory N140 component was elicited after synchronous, compared with uncorrelated, visuo-tactile training, independently of the previously viewed object (rubber hand or neutral object), suggesting that this early effect is modulated by temporal contiguity, but not by pre-existing body-representations (see also Keysers et al., 2004). Interestingly, ERP modulations observed beyond 200 ms post-stimulus showed a different pattern. During the 200–450 ms post-stimulus interval, an enhanced sustained negativity was generally found for trials where a tactile stimulus was presented to the hand that was anatomically compatible with the visible rubber hand/object, relative to trials where the incompatible hand was stimulated instead, after synchronous training, but not after training with uncorrelated multisensory stimulation. On the contrary, when participants saw a neutral object, enhanced sustained negativity was present following blocks of both synchronized and uncorrelated visuo-tactile training. This pattern reflects attentional modulation by specific mental representation of the body (Press et al., 2008), suggesting that the compatibility between the visual form of the stimulus and an anatomical representation of the body specifically modulates attentional processing of tactile stimuli at post-perceptual processing levels, over and above the synchronicity of multisensory input.

Based on neuropsychological symptoms following lesions in the right temporal and parietal lobes (Berlucchi & Aglioti, 1997; Bottini, Bisiach, Sterzi, & Vallar, 2002; Frassinetti, Maini, Romualdi, Galante, & Avanzi, 2009; Fotopoulou et al., 2008; Moret et al., 2003), Tsakiris et al. (2008) hypothesized that disrupting activity in the right temporoparietal junction (rTPJ) would impair the process that tests for the compatibility between the visual form of the stimulus and a mental representation of the body on the basis of visuo-tactile evidence. Single-pulse transcranial magnetic stimulation (TMS) was delivered 350 ms after synchronous visuo-tactile stimulation of the participant’s own hand and a rubber hand, or the participant’s own hand and a neutral object. rTPJ was determined on the basis of anatomical landmarks, defined as the junction of the supramarginal, angular, and superior temporal gyri. Proprioceptive drift was used as a behavioural proxy of the RHI. Overall, TMS over rTPJ reduced the extent to which the rubber hand was incorporated into the mental representation of one’s own body, while it increased the incorporation of a neutral object, as measured by the proprioceptive drift towards or away from the viewed object. A corporeal object (i.e. a rubber hand) that would normally have been perceived as part of the subject’s own body was no longer significantly distinguished from a clearly neutral object, suggesting that the disruption of neural activity over rTPJ blocked the contribution of the body-model in the assimilation of current sensory input, making the discrimination between what may or may not be part of one’s body ambiguous. This effect of TMS over rTPJ seems to have impaired a body/non-body discrimination process. This specific test-for-fit process can be used to filter visual and tactile events that may be assigned to one’s own body, from sensory events that produce a mismatch. This view also resonates with a recent hypothesis about the computational process implemented in the rTPJ. Based on a meta-analysis of neuroimaging studies reporting activations of rTPJ in various tasks (e.g. self-recognition, agency, theory of mind, attention reorientation, perspective-taking), Decety and Lamm (2007) suggested that the rTPJ may underpin a single computational mechanism that is used by multiple cognitive processes; this mechanism involves the comparison of internal states (e.g. prediction and representations of the body or the self in more general) with external sensory events. This basic computational mechanism would be important for self-world interactions (e.g. detection of multisensory mismatch, agency), but also for higher cognitive functions involved in self-other interactions.
6.2. Body-related multisensory integration: the contribution of parietal and premotor cortices

Once the external object passes the test-for-fit, then synchronized visuo-tactile stimulation can drive the induction of the RHI as a necessary condition. If there is a congruency between the posture and spatial location of the two hands, processes of multisensory integration in peri-hand space will allow for the recalibration of the visual and tactile coordinate systems, leading to the eventual referral of the tactile sensation to the vision of touch delivered on the rubber hand. 

Ehrsson et al. (2004), Ehrsson, Holmes, and Passingham (2005) and Ehrsson et al. (2007) showed bilateral neural activity in the ventral premotor cortex (PMv) and posterior parietal cortex (PPC) in the conditions that induced the RHI. Consistent findings in these three fMRI studies suggest different roles for posterior parietal cortex and PMv during the RHI. According to Makin et al. (2008), the PPC seems to integrate multisensory information with respect to the rubber hand. This integration starts before the onset of the RHI (<11.3, 70.5 s, the stable period when people experience the illusion and rCBF was observed in the contralateral (left) primary and secondary somatosensory cortices. A small or negative proprioceptive drift in the RHI studies indicates that the rubber hand has not been attributed to one’s own body (Botvinick & Cohen, 1998; Longo et al., 2008). In these situations, the representation of the current state of the body is not captured by visual input because of the discrepancy. A possible role of somatosensory cortex activation relates to the salience of the representation of the subject’s own hand when the pattern of multisensory stimulation does not support the incorporation of the rubber hand: for example, when the visuo-tactile stimulation is asynchronous or when the rubber hand is anatomically incongruent with respect to the participant’s hand. The maintenance of the current state of the body in the somatosensory cortex would prevent the induction of the RHI by making the participant’s hand representation salient so that it becomes resistant to multisensory stimulation. Somatosensory cortex activations are sensitive to handedness (i.e., left- vs. right-hand manipulation) and related anatomic constrains (see also Costantini et al., 2005), to the kinaesthetic proprioceptive space (i.e., proprioceptive drift), and to both visual and tactile inputs (see also Schaefer, Flor, Heinze, & Rotte, 2006; Schaefer, Heinze, & Rotte, 2005; Schaefer, Noennig, Heinze, & Rotte, 2006). Thus, the somatosensory cortex may be involved in the processing of the current body state that includes anatomical and postural representations (see Fig. 1, comparison 2).

The experience of ownership of the rubber hand as measured by proprioceptive drifts was positively correlated with activity in the right posterior insula. Right insular activity is consistently implicated in self-attribution (Farrer & Frith, 2002), self-processing (Fink et al., 1996; Vogele, et al., 2004), and the representation of an egocentric reference frame. The roles of the insular lobe for body-awareness in general (Craig, 2002, 2009), and of the right posterior insula in particular for egocentric representation (Fink et al., 2003), agency (Farrer et al., 2003), self-recognition (Devue et al., 2007) and body-ownership (Baier & Karnath, 2008) are well supported by recent studies. The hypothesis that the right posterior insula is linked to the experience of body-ownership is also supported by available evidence on somatoparaphrenia. A first lesion mapping study suggested that the right posterior insula is commonly damaged in patients with anosognosia for hemiplegia (AHP), but is significantly less involved in hemiplegic patients without AHP (Karnath, Baier, & Nagele, 2005; see also Berti et al., 2005; Cereda, Ghika, Maeder, & Bogousslavsky, 2002). A more recent lesion mapping study that focused specifically on patients with somatoparaphrenic symptoms (Baier & Karnath, 2008) revealed...
that the right posterior insula is indeed the critical structure involved in phenomena of “disturbed sensation of limb ownership”. Two further insights from the literature on somatoparaphrenia are particularly relevant for the understanding of induced body-ownership in the RHI. First, as the review by Vallar and Ronchi (2009) suggests, patients with spared proprioception do not exhibit somatoparaphrenia. The hypothesis that proprioceptive impairment is of central role in breakdowns of ownership is particularly interesting in relation to the behavioural measure used to quantify ownership in the RHI.2 Second, Vallar and Ronchi (2009) point to the fact that on the basis of the available case studies to date, one main feature of somatoparaphrenia may be a blurred distinction between corporeal and extracorporeal objects. This observation points to the critical role of the body-model in maintaining a coherent sense of one’s body.

6.4. A neural network for body-ownership

Overall, the brain processes that produce the sense of body-ownership depend on current sensory integration and on the contribution of internal models of the body. The right temporoparietal junction may underpin the assimilation of novel multisensory signals by maintaining a pre-existing reference representation of one’s own body. The rTPJ may underpin decisions about the incorporeality of the viewed object in relation to a reference body-model (see Tsakiris et al., 2008, and comparison 1 in Fig. 1). The primary and associative somatosensory cortices seem to maintain on-line anatomical and postural representations of the current state of the body against which the anatomical and postural features of the stimulated object are compared (see comparison 2, Fig 1). Body-related sensory integration linked to the onset of body-ownership during the RHI is related to activity in the posterior parietal cortex and the ventral premotor cortex (see comparison 3, Fig 1, and Ehrsson et al., 2004, 2007; Kammers et al., 2008). The effect of multisensory integration and recalibration of hand position, namely the experience of body-ownership of the rubber hand, is correlated with activity in the right posterior insula (Tsakiris, Hesse et al., 2007; Tsakiris, Schütz-Bosbach et al., 2007; see also Baier & Karnath, 2008). Other authors have also suggested that the insula is concerned with higher order somatosensory processing of the body that is related to subjective awareness and affective processing of bodily signals (Craig, 2002, 2009; Dijkerman & de Haan, 2007). The available imaging evidence on the RHI are consistent with the view that SII and the insula are responsible for conscious somatosensory perception, with the right posterior parietal cortex contributing to spatio-temporal integration (Dijkerman & de Haan, 2007). Circuitry and connectivity analyses demonstrate both the afferent and efferent connectivity of the insula with SII, the temporoparietal area and the premotor cortex (Augustine, 1996; see also Dijkerman & de Haan, 2007). These structures may form a network that plays a fundamental role in linking current sensory stimuli to one’s own body, and thus also in self-awareness. The available neuroimaging and neuropsychological data favour a right-hemispheric specificity for self-processing in general (see Keenan, Rubio, Racioppo, Johnson, & Barnacz, 2005) and for body-ownership specifically (Baier & Karnath, 2008; Tsakiris, Hesse et al., 2007; Tsakiris, Schütz-Bosbach et al., 2007; Vallar & Ronchi, 2009).

7. Beyond my hand: my body and myself

This paper focused on the necessary conditions for the experience of a body-part as belonging to my body as studied with the RHI. Blanke and Metzinger (2009) rightly comment on the need to investigate a more “global” sense of body-ownership for the whole body. Three recent studies employed visuo-tactile synchrony to investigate the extent to which phenomena similar to the RHI can be induced for whole bodies. Ehrsson (2007) used synchronous or asynchronous visuo-tactile stimulation while participants were looking at their back with the perspective of a person sitting behind them with stereoscopic vision. Synchronous but not asynchronous visuo-tactile stimulation induced a shift in the 1st person-perspective such that participants experienced being located at some distance behind the visual image of their own body as if they were looking at someone else. In the study by Lenggenhager et al. (2007), participants viewed the backs of their bodies filmed from a distance of 2 m and projected onto a three-dimensional (3D)-video head-mounted display. The participants’ backs were stroked either synchronously or asynchronously with respect to the virtually seen body. Questionnaire ratings and a behavioural measure analogous to proprioceptive drift in the RHI shall not only after synchronous stimulation, participants felt as the virtual body was their body. Similar results were obtained when participants saw a virtual fake body (e.g. a mannequin), but not when participants saw a virtual non-corporeal object, replicating other studies reporting an abolishment of the illusion of ownership for non-corporeal objects (see Haans et al., 2008; Tsakiris & Haggard, 2005). Interestingly, the necessary conditions for the experience of ownership over a body-part seem to be the same as the ones involved in the experience of ownership for whole bodies. The question of whether ownership for body-parts has different functional correlates from ownership for the whole body has not been directly addressed in the empirical literature. However, the available empirical findings from the two domains suggest that very similar neurocognitive processes are involved in ownership of body-parts and bodies.

Two further manipulations of the whole-body studies resulted in the illusion of body-swapping (Petkova & Ehrsson, 2008) and changes in self-face recognition (Tsakiris, 2008). Petkova and Ehrsson (2008) fitted two small cameras on the head of a mannequin directed downwards. The image from the two cameras was projected to a head-mounted display worn by the participant. When the participant looked downwards, she saw the mannequin’s body, where she would normally expect to see her own. Synchronous visuo-tactile stimulation induced the illusion of being this other body (i.e. the mannequin’s body), suggesting that multisensory stimulation can induce not only an analogue of out-of-body experiences (Ehrsson, 2007; Lenggenhager et al., 2007), but also an illusion of being into another body and a dramatic change in embodied perspective. These manipulations demonstrate the efficiency of current multisensory input in determining the experience of a minimal 1st person-perspective (Ehrsson, 2007), self-location (Lenggenhager et al., 2007) and self-identification (Petkova & Ehrsson, 2008), three conditions that are critical for the experience of selfhood (Blanke & Metzinger, 2009). To further investigate the extent to which current multisensory input may influence the sense of self-identity, Tsakiris (2008) extended the paradigm of multisensory integration to self-face recognition. Participants were stroked on their face while they were looking at a morphed face being touched in synchrony or asynchrony. Before and after the visuo-tactile stimulation participants performed a self-recognition task. The results showed that synchronized multisensory signals had a significant effect on self-face recognition. Synchronous tactile stimulation while watching another person’s face being similarly touched produced a bias in recognizing one’s own face, in the direction of the other person included in the representation of one’s own face. This effect provides direct evidence that our mental representation of our self, such as self-face representation, is not solely derived from stable representations, but instead these

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2 Obviously, loss of proprioception by itself is by no means sufficient for breakdowns in body-ownership as the literature on de-afferented patients suggests.
representations are susceptible to current multisensory evidence. Multisensory integration can update cognitive representations of one’s body, such as the sense of ownership of body-parts (Longo et al., 2008) or whole body (Ehrsson, 2007; Lenggenhager et al., 2007; Petkova & Ehrsson, 2008), the physical appearance of one’s body (Longo et al., 2009), and the representation of one’s identity in relation to other people (Tsakiris, 2008).

8. Conclusion

One of the key questions in the neurocognitive study of self is that of specificity (Gillihan & Farah, 2005; Legrand & Ruby, 2009). Gillihan and Farah (2005) point to the fact that there is not a self-specific neural system or a single sense of self. Legrand and Ruby (2009) suggest that “self-specificity characterizes the subjective perspective, which is not intrinsically self-evaluative but rather relates any represented object to the representing subject”, by means of multisensory processing and sensorimotor integration. The present review focused on multisensory processing and its role for body-ownership only (for the role of sensorimotor integration for body-ownership, see Tsakiris, Schütz-Bosbach, & Gallagher, 2007). In particular, it considered how multisensory integration together with internal models of the body modulate the experience of the body as being one’s own, as well as the demarcation or distinction between one’s body and other objects. The experience of body-ownership may represent a critical component of self-specificity as evidenced by the different ways in which multisensory integration in interaction with internal models of the body can actually manipulate important physical and psychological aspects of the self. Future studies should further investigate the neurocognitive processes that bridge physical and psychological dimensions of self to advance our understanding of the sense of identity.

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References


Lloyd, D. M. (2007). Spatial limits on referred touch to an alien limb may reflect
Kammers, M. P., Verhagen, L., Dijkerman, H. C., Hogendoorn, H., de Vignemont, F.,
Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: Perceptual illusion of body
Journal of Cognitive Neuroscience. [Epub ahead of print].