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

Manos Tsakiris
Department of Psychology, Royal Holloway, University of London
Egham, Surrey, TW20 0EX, UK
Email : manos.tsakiris@rhul.ac.uk

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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 many 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 online 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 Synfozik, Vosgerau & Neuen, 2008; Tsakiris, Schutz-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 et al., 1999; Tsakiris et al., 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, Vosgerau & Neuen, 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 misolocalizations 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 illusion over time (Botvinick & Cohen, 1998) and the subjective intensity of the experience of body-ownership (Longo et al, 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 replications (Armel & Ramachandran, 2003; Ehrsson et al., 2004; Longo et al., 2008; Tsakiris & Haggard, 2005; Tsakiris et al., 2007) and modifications of the classic paradigm (Austen et al., 2004; Capelari et al., 2009; Durgin et al, 2007; Ehrsson, 2007; Ehrsson et al, 2007,2008; Hägni et al., 2008; Kammers et al., 2009; Kanayama, Sato & Ohira, 2007, 2008; Lenggenhager et al, 2007; Petkova & Ehrsson, 2008; Schütz-Bosbach et al., 2006, 2009; Slater et al., 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 processe, 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 et al, 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 is 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 suggests 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 on the basis of sensory stimulation. 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 towards the spatial location of the visual percept. Botvinick and Cohen (1998) put forward a bottom-up explanation of the RHI by suggesting that intermodal matching between vision and touch is *sufficient* for self-attribution of the rubber hand. The first RHI studies showed the presence of synchronized visual and tactile stimulation to be a *necessary* condition for the inducement of the RHI, since RHI did not occur after asynchronous stimulation (Botvinick & Cohen, 1998; Ehrsson et al., 2004; Tsakiris & Haggard, 2005). But does this make intermodal matching sufficient for the experience of body-ownership?

Armel and Ramachandran (2003) held a strong version of the Botvinick and Cohen view by arguing that visuo-tactile correlation is both necessary and sufficient condition for the RHI: any object can be experienced as part of one's body if the appropriate intermodal matching is present. If after the synchronous visuo-tactile stimulation period, the experimenter "injured' the rubber 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; de Vignemont, Tsakiris & Haggard, 2006; Dijkerman & de Haan, 2007; Graziano & Botvinick, 2001; Carruthers, 2008; Holmes & Spence, 2006; Sirigu et al., 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 form of a reference 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 & Botvinick (2001), body

[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 Ramachadran (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 ($p=0.05$).

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. 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-corporeal 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-corporeal object such a wooden stick (i.e. coding of visual form representations of body-parts, Haans, Ijsselsteijn & de Kort, 2008; Tsakiris & Haggard 2005; Tsakiris, Costantini & Haggard 2008, see also Holmes, Snijders, & Spence, 2006; see also Graziano, Cooke and Taylor 2000, but cf. Armel and 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 & 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 & Ramachadran (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 & Haggard, 2005; Tsakiris et al., in press). 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 no experience of ownership is 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 and Haggard 2007; Tsakiris and Haggard 2005, see also Graziano, Cooke and Taylor 2000; Pavani, Spence and Driver 2000; but cf. Armel and 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 and 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 30cm. 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 (<27.5cm), 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 & 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 (Costanini & Haggard, 2007; Lloyd, 2007; Ehrsson et al., 2004; 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 & Erhsson (2008) put forward a parsimonious account of the RHI based on processes of multi-sensory 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 multi-sensory hand-centred representations of space (Lloyd, 2007; Makin, Holmes & Erhsson, 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 & Haggard, 2007), or when the viewed object is not a body-part (e.g. a neutral non-corporeal object).

Mechanisms of hand-centred multisensory integration operate during body-extension after use of non-corporeal objects (e.g. tool-use, see Maravita & Iriki, 2004) as well as during incorporation (Ehrsson et al. 2004), suggesting that they perform a basic computational process that is not unique to body-ownership. In fact, the mechanisms of peri-hand multisensory integration implicated by Makin et al (2008) in the experience of body-ownership are present even if there is a postural incongruency between the participant's own hand and the rubber hand:

for example the preference for a stimulus approaching the rubber hand is similar in the posterior part of the intraparietal sulcus to that shown for the real hand (Makin et al, 2007), suggesting that viewing visual stimuli near a rubber hand is sufficient to change the representation of hand position in peri-hand brain areas. However, even small incongruencies at the postural level abolish the RHI (Costantini & Haggard, 2007).

In addition, lesions in brain areas that underpin these processes such as the ventral premotor cortex and intraparietal sulcus (Makin, Holmes & Ehrsson, 2008) do not result in denial of body-ownership (Baier & Karnath, 2007). Makin, Holmes & Ehrsson (2008) cite two studies by Arzy et al (2006) and Berti et al (2007) 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 asomatognosia (i.e. loss of awareness of one body-half (which may or may be not paralysed, see Critchey, 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 and colleagues (2007) focused on patients with anosognosia for hemiplegia, a syndrome that is dissociable from somatoparaphrenia (Vallar & Rocheti, 2008). 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 multi-sensory integration in peri-hand space, without considering other higher-order representations of the body.

The aforementioned processes postulated by Makin, Holmes & Ehrsson (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 (Tsakiris & Haggard, 2005; Haans et al., 2008; see also Holmes, Snijders, & Spence, 2006), the anatomical congruency between viewed and felt body-part (Tsakiris & Haggard, 2005; Graziano et al., 2000; Pavani et al, 2000), 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; Tsakiris & Haggard, 2005; Costantini & Haggard, 2007; Ehrsson et al., 2004; Pavani et al., 2000), and the spatial relation between viewed and felt body-part (Lloyd, 2007), modulate the induction of the RHI and the experience of body-ownership. Figure 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 (Tsakiris, Haggard & Costantini, 2008; Costantini and Haggard 2007; Tsakiris and Haggard 2005), that are diachronic, in contrast to the body schema which is continuously updated as the body moves (Wolpert et al. 1998). Other authors have suggested the existence of a stored and not stimulus-evoked body-structural description that would contain representations about (a) the shape and contours of the human body, (b) a detailed plan of the body surface, (c) the location of body-parts, the boundaries between them, and their internal part-relation (de Vignemont, Tsakiris & Haggard, 2004; Schwoebel & Coslett, 2005). Schwoebel and Coslett (2005) suggested that this body-structural description is view-independent or even allocentric, but what seems to be important for the sense of body-ownership induced during the RHI is that the body-model operates off-line and more interestingly it seems to be normative (de Preester & Tsakiris, 2009) or egopetal (Longo et al., 2009) for one's own body, because its modulatory influence allows for an external body-part to be considered as a potential part of *my* body or not. This first critical comparison will test the fitness for incorporeability of the viewed object. Objects that do not pass this test will not be experienced as part of one's body even if visuo-tactile stimulation is synchronous (Haans et al., 2008; Tsakiris, Costantini & Haggard, 2008; Tsakiris & Haggard, 2005; but see Armel & Ramachadran, 2003). The model predicts that the more the viewed object matches the structural appearance of the body-part's form, the stronger the experience of body-ownership will be. Features such as skin colour do not seem to enter into this comparison (see Longo et al., 2009) and this is a further argument why this body-model should not be equated with a conscious body-image.

The second critical comparison takes place between the current state of the body and the postural and anatomical features of the body-part that is to be attributed. Body schematic processes (e.g. current postural configuration), as well as current reafferent information (as shown in the connection between touch and vision and body state in Figure 1) will be informing this current state of the body. If there is incongruency 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 and the eventual feeling of body-ownership (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005) that updates the body-model. 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.

INSERT FIGURE 1 AROUND HERE

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 online internal models of the body (Tsakiris and Haggard, 2005; Tsakiris, 2007). 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., 2007; Tsakiris et al., 2007) and posterior parietal cortices (Ehrsson et al, 2004; Kammers et al., 2008; Makin, Holmes & Ehrsson, 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 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., 2007) 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, Costantini & Haggard (2008) suggested that current sensory stimuli are processed and finally tested-for-fit against an abstract body-model that maintains a coherent sense of one's body as distinct from other non-corporeal objects (see Figure 1, comparison 1).

Press et al (2007) investigated whether the modulation of somatosesnsory processing by visuotactile 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 visuotactile training. An enhanced somatosensory N140 component was elicited after synchronous, compared with uncorrelated, visuotactile 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 200ms post-stimulus showed a different pattern. During the 200-450ms 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 o, 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 visuotactile 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 ((Bottini et al. 2002; Mort et al. 2003; Berlucchi and Aglioti 1997; Frassinetti et al, 2008;Fotopoulou et al., 2008), Tsakiris et al. (2008) hypothesized that disrupting activity in the right temporo-parietal junction (rTPJ) would impair the process the 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 350ms 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. An 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-recogniton, agency, theory of mind, attention reorientation, perspective-taking), Decety & 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 self-world interactions (e.g. detection of multisensory mismatch, agency), but also for higher cognitive functions involved in self-other interactions .

<u>6.2. Body-related multisensory integration: the contribution of parietal and premotor cortices</u>

Once the external object passes the test-for-fit, then synchronized visuo-tactile stimulation can drive the inducement of the RHI as a necessary condition. If there is a congruency between the posture and spatial location of the two hands, processes of multi-sensory 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 and colleagues (2004, 2005, 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 three fMRI studies suggest different roles for posterior parietal cortex and PMv during the RHI. According to Makin, Holmes & Ehrsson (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, ± 7.0 sec, from Ehrsson et al, 2004), suggesting that PPC is involved in the resolution of the conflict between the incoming visual and tactile information, and the resulting recalibration of the visual and tactile coordinate systems (see Figure 1, comparison 3).

Another area of interest in the parietal cortex is the inferior parietal lobule (IPL). IPL has been shown to play a critical role in representing spatial relations of body-parts (Buxbaum &

Coslett, 2001). More recently, Dijkerman & de Haan (2007) suggested that the IPL may process information related to perceptual judgments about body configuration. Kammers et al (2008) used off-line low-frequency repetitive transcranial magnetic stimulation (rTMS) to investigate the role of the inferior posterior parietal lobule (IPL) in the inducement of the RHI. The left IPL was targeted over the P3 electrode site, according to the International 10–20 EEG System. Results showed that rTMS over the IPL attenuated the strength of the RHI as measured by proprioceptive drift, while subjective self-reports of feeling of ownership over the rubber hand remained unaffected by rTMS. This finding suggests that perhaps the recalibration of the visual and tactile coordinate systems is not sufficient for the experience of ownership. As Kammers et al (2008) note, the RHI may influence the experience and localization of one's own hand in an independent manner (see also Longo et al., 2009 for the partly independent components of ownership and localization of hand assessed with introspective evidence). In addition, proprioceptive mislocalizations can be observed in the absence of experienced ownership (Holmes, Snijders, & Spence, 2006). However, under conditions that elicit the sense of body-ownership during the RHI, the felt location of one’s hand towards or away from the viewed object in the classic RHI manipulations has been shown to correlate with the sense of body-ownership (Botvinick & Cohen, 1998; Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008), suggesting that proprioceptive drifts can be used as a behavioural proxy of the ownership: proprioceptive drifts towards the viewed object during the RHI indicate incorporation and experienced ownership, while proprioceptive drifts away from the viewed object indicate failure of incorporation and disownership.

Regarding the contribution of premotor cortex, as Makin, Holmes & Ehrsson (2008) note, the PMv shows additional multisensory responses during the period when people experience the illusion (between 11.3 and 42 sec). This supra-additive activation could be explained by the enhancement of the responses of bimodal neurons once their reference frame is centred on the rubber hand, and participants start referring the touch to the rubber hand as a result of binding the visual and tactile events in hand-centred coordinates in the PPC. Thus, when the illusion starts, the hand-centred reference frames shift from the participant’s hidden hand to the rubber hand. This shift is accompanied by a recalibration of the participant’s hand position (i.e. proprioceptive drift), and it results in the referral of the tactile sensation to the rubber hand. Note, however, that visuo-tactile correlation generates particularly strong proprioceptive drifts towards the rubber hand during the first 60sec, implying that the hand-centred reference frames continue to shift towards the rubber hand, and that the referred sensations are enhanced during that period. After 1 minute of stimulation, the recalibration of hand position increases in a less exponential manner for up to 3 min (see experiment 4 in Tsakiris & Haggard, 2005). It therefore remains unknown whether activity in the PMv between 11.3 and 42 sec in Ehrsson et al (2004) reflects this rapid recalibration of hand position or the referral of tactile sensation on the rubber hand which could arise as an effect, rather than as cause, of the recalibration.

6.3. The subjective experience of body-ownership: the role of the right insular lobe

Tsakiris et al (2007) used Positron Emission Tomography (PET) to detect sustained neural activity that was specifically related to the stable state of ownership of the rubber hand, and not to the onset of the RHI per se (i.e. the period of recalibration of the visual and tactile coordinate systems and touch referral). A negative correlation between the proprioceptive measure of the illusion and rCBF was observed in the contralateral (right) 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 et al. 2005; Schaefer, Flor, et al. 2006; Schaefer, Noennig, et al. 2006). Thus, the somatosensory cortex may be involved in the processing of the current body state that includes anatomical and postural representations (see Figure 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; Vogeley 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 & Naagele, 2005; see also Cereda et al., 2002; Berti et al., 2005). 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. As the review by Vallar & Ronchi (2008) 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 (2008) 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 both on current sensory integration and also on the contribution of internal models of the body. The right temporo-parietal 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 incorporeability of the visual form of the viewed object with a reference body-model (see Tsakiris, Costantini & Haggard; 2008, and comparison 1 in Figure 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, Figure 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, Figure1, 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

[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.

rubber hand, is correlated with activity in the right posterior insula (Tsakiris 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 a 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 Djikerman & de Haan, 1997). 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 et al., 2005) and for body-ownership specifically (Baier & Karnath, 2008; Tsakiris et al., 2007; Vallar & Ronchi, 2008).

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 & 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 Leggenhanger 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 showed that 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 full 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 & 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; Leggenhager 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 (Leggenhager 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 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; Leggenhanger 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).

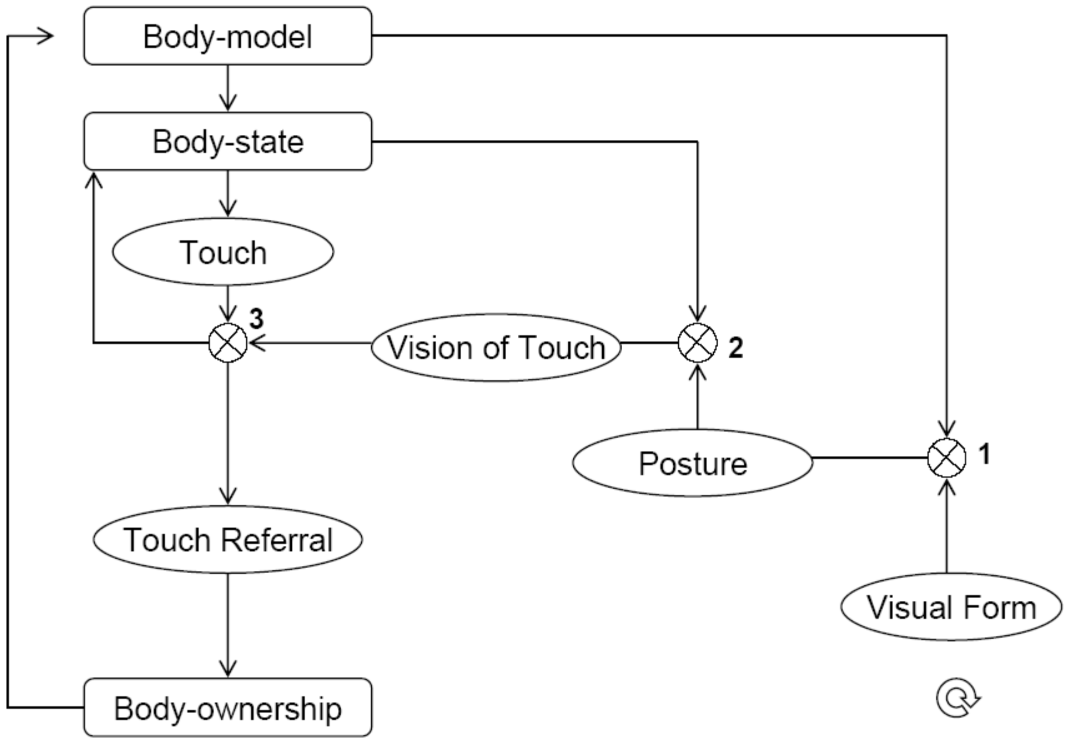
8. Conclusion

One of the key questions in the neurocognitive study of self is that of specificity (Gillihan & Farah, 2005; Legrand & Ruby, 2009). Gillihan & Farah (2004) point to the fact that there is not a self-specific neural system or a single sense of self. Legrand & 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, Schutz-Bosbach & Gallagher, 2008). 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.

Figure Caption

Figure 1: A neurocognitive model of body-ownership during the Rubber Hand Illusion. 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. The rTPJ has been shown to be involved in this comparison (Tsakiris, Haggard & Costantini, 2008). The second critical comparison takes place between the current state of the body and the postural and anatomical features of the body-part that is to be experienced as mine. This comparison is underpinned by activity in anterior parietal areas such as the primary and secondary somatosensory cortices (see Press et al., 2007; Tsakiris 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, Holmes & Ehrsson, 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 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.

Figure 1


Body-model
Body-state
Touch
3
Vision of Touch
2
Posture
1
Touch Referral
Visual Form
Body-ownership

References

Armel, K. C., & Ramachandran, V. S. (2003). Projecting sensations to external objects: evidence from skin conductance response. *Proceedings of the Royal Society London B Biological Sciences, 270*, 1499–1506.

Arzy S, Overney LS, Landis T, Blanke O. (2006) Neural mechanisms of embodiment: asomatognosia due to premotor cortex damage. *Archives of Neurology, 63*,1022–5.

Augustine JR. (1996). Circuitry and functional aspects of the insular lobe in primates including humans. *Brain Research: Brain Research Reviews, 22*,229-244.

Austen EL, Soto-Faraco S, Enns JT, Kingstone A. (2004) Mislocalisation of touch to a fake hand. *Cognitive, Affective, & Behavioral Neuroscience, 4*,170–181.

Baier B, Karnath HO.(2008)Tight link between our sense of limb ownership and self awareness of actions. *Stroke , 39*, 486–8.

Berlucchi G, Aglioti S (1997) The body in the brain: neural bases of corporeal awareness. *Trends in Neuroscience, 20*, 560-564.

Berti A, Bottini G, Gandola M, Pia L, Smania N, Stracciari A, Castiglioni I, Vallar G, Paulesu E. (2005) Shared cortical anatomy for motor awareness and motor control. *Science, 309*, 488-91.

Blanke O, Metzinger T. (2009) Full-body illusions and minimal phenomenal selfhood. *Trends in Cognitive Sciences, 13*, 7-13.

Blanke O, Ortigue S, Landis T, Seeck M. (2002). Stimulating illusory own-body perceptions. *Nature, 419*, 269

Bottini G, Bisiach E, Sterzi R, Vallarc G (2002) Feeling touches in someone else's hand. *Neuroreport 13*, 249-252.

Botvinick M, Cohen J (1998) Rubber hands 'feel' touch that eyes see. *Nature 391*, 756.

Buxbaum, L. J., & Coslett, H. B. (2001). Specialised structural descriptions for human body parts: Evidence from autotopagnosia. *Cognitive Neuropsychology, 18*, 289–306.

Capelari ED, Uribe C, Brasil-Neto JP. (2009) Feeling pain in the rubber hand: integration of visual, proprioceptive, and painful stimuli. *Perception.38*, 92-9.

Carruthers, G. (2008). Types of body representation and the sense of embodiment. *Consciousness & Cognition. 17*, 1302-1316.

Cereda,C., Ghika,J., Maeder,P., and Bogousslavsky,J. (2002). Strokes restricted to the insular cortex. *Neurology 59*, 1950-1955.

Craig AD. (2002) How do you feel? Interoception: the sense of the physiological condition of the body. *Nature Reviews Neuroscience,3*, 655-66.

Craig AD.(2009) How do you feel--now? The anterior insula and human awareness. *Nature Reviews Neuroscience. 10*, 59-70.

Critchley M (1953) *The parietal lobes*. Hafner, New York

Costantini M, Haggard P. (2007) The rubber hand illusion: sensitivity and reference frame for body ownership. *Consciousness & Cognition, 16*, 229–40.

Costantini M, Galati G, Ferretti A, Caulo M, Tartaro A, Romani GL, Aglioti SM. 2005. Neural systems underlying observation of humanly impossible movements: an FMRI study. *Cerebral Cortex, 15,* 1761-1767.

Daprati E, Franck N, Georgieff N, Proust J, Pacherie E, Dalery J & Jeannerod M (1997), Looking for the agent: an investigation into consciousness of action and self-consciousness in schizophrenic patients. *Cognition, 65,* 71-86.

Decety, J., & Lamm, C. (2007). The role of the right temporoparietal junction in social interaction: How low-level computational processes contribute to metacognition. *The Neuroscientist: A Review Journal Bringing Neurobiology, Neurology and Psychiatry, 13,* 580–593.

De Preester H & Tsakiris M (2009) Body-extension versus body-incorporation: Is there a need for a body-model?. *Phenomenology & Cognitive Sciences*, in press

De Vignemont F (2007) Habeas Corpus: The Sense of Ownership of One's Own Body. *Mind & Language, 22*, 427-449

De Vignemont F, Tsakiris, M & Haggard P (2005), ‘Body Mereology’. In G. Knoblich, I. Thornton, M. Grosjean, & M. Shiffrar (Eds.), *Human Body Perception from the Inside Out*. NY: Oxford University Press.

di Pellegrino, G., Ladavas, E., & Farne, A. (1997). Seeing where your hands are. *Nature, 388*, 730.

Devue C, Collette F, Balteau E, Degueldre C, Luxen A, Maquet P, et al. (2007) Here I am: the cortical correlates of visual self-recognition. *Brain Research, 1143,*169–82.

Dijkerman HC, de Haan EH.(2007) Somatosensory processes subserving perception and action. *Behavioural Brain Science , 30,* 189-201;

Durgin FH, Evans L, Dunphy N, Klostermann S, Simmons K. (2007) Rubber hands feel the touch of light. *Psychological Science, 18*, 152-7.

Ehrsson HH (2007). The experimental induction of out-of-body experiences. *Science, 317*, 1048.

Ehrsson HH, Rosén B, Stockselius A, Ragnö C, Köhler P, Lundborg G.(2008) Upper limb amputees can be induced to experience a rubber hand as their own. *Brain. 131*, 3443-52.

Ehrsson HH, Holmes NP, Passingham RE. (2005) Touching a rubber hand: feeling of body ownership is associated with activity in multisensory brain areas. *Journal of Neuroscience, ;25*, 10564–73.

Ehrsson HH, Spence C, Passingham RE. (2004). That's my hand! Activity in premotor cortex reflects feeling of ownership of a limb. *Science*, *305*, 875–7.

Ehrsson HH, Wiech K, Weiskopf N, Dolan RJ, Passingham RE. (2007) Threatening a rubber hand that you feel is yours elicits a cortical anxiety response. *Proceedings of the National Academy of Sciences, 104*, 9828–33.

Farne, A., Dematte, M. L., & Ladavas, E. (2005). Neuropsychological evidence of modular organization of the near peripersonal space. *Neurology*, *65*, 1754–1758.

Farrer C, Frith CD (2002) Experiencing Oneself vs Another Person as Being the Cause of an Action: The Neural Correlates of the Experience of Agency. *NeuroImage 15*, 596-603.

Farrer C, Franck N, Georgieff N, Frith CD, Decety J, Jeannerod M (2003a) Modulating the experience of agency: a positron emission tomography study. *NeuroImage 18*, 324-333.

Fink,G.R.,Markowitsch,H.J., Reinkemeier,M., Bruckbauer,T., Kessler,J., and Heiss,W.D. (1996). Cerebral representation of one's own past: neural networks involved in autobiographical memory. *Journal of Neuroscience*, *16*, 4275-4282.

Fink,G.R., Marshall,J.C., Weiss,P.H., Stephan,T., Grefkes,C., Shah,N.J., Zilles,K., and Dieterich,M. (2003). Performing allocentric visuospatial judgments with induced distortion of the egocentric reference frame: an fMRI study with clinical implications. *Neuroimage 20*, 1505-1517.

Fotopoulou A, Tsakiris M, Haggard P, Vagopoulou A, Rudd A, Kopelman M. (2008) The role of motor intention in motor awareness: an experimental study on anosognosia for hemiplegia. *Brain, 131*, 3432-42

Franck N, Farrer C, Georgieff N, Marie-Cardin M, Dalery J, d'Amato T & Jeannerod M (2001). Defective recognition of one's own actions in patients with schizophrenia. American *Journal of Psychiatry, 158,* 454-459.

Frassinetti F, Maini M, Romualdi S, Galante E, Avanzi S.(2009) Is it mine? Hemispheric asymmetries in corporeal self-recognition. *Journal of Cognitive Neuroscience, 20,*1507-16.

Gallagher S (2000). Philosophical concepts of the self: implications for cognitive sciences. *Trends in Cognitive Sciences 4*, 14-21.

Gillihan SJ & Farah MJ (2005). Is self special? A critical review of evidence from experimental psychology and cognitive neuroscience. *Psychological Bulletin, 131*, 76-97.

Graziano, M. S., Cooke, D. F., & Taylor, C. S. (2000). Coding the location of the arm by sight. *Science, 290*, 1782–1786.

Graziano,M. S. A. and Botvinik, M. M. (2001) How the brain represents the body: insights from neurophysiology and psychology. In Prinz,W. and Hommel, B. (eds), *Common Mechanisms in Perception and Action, Attention and Performance XIX*. Oxford University Press, Oxford/New York.

Haans A, Ijsselsteijn WA, de Kort YA. (2008) The effect of similarities in skin texture and hand shape on perceived ownership of a fake limb. *Body Image, 5*(4):389-94.

Hägni K, Eng K, Hepp-Reymond MC, Holper L, Keisker B, Siekierka E, Kiper DC. (2008) Observing virtual arms that you imagine are yours increases the galvanic skin response to an unexpected threat. *PLoS ONE. 3*(8):e3082

Hari,R., Hanninen,R., Makinen,T., Jousmaki,V., Forss,N., Seppa,M., and Salonen,O. (1998). Three hands: fragmentation of human bodily awareness. *Neuroscience Letters. 240*, 131-134.

Holmes, N. P., Snijders, H. J., & Spence, C. (2006). Reaching with alien limbs: Visual exposure to prosthetic hands in a mirror biases proprioception without accompanying illusions of ownership. *Perception and Psychophysics, 68*, 685–701.

Holmes, NP.; Spence, C. (2006) Beyond the body schema: Visual, prosthetic, and technological contributions to bodily perception and awareness. In: Knoblich, G.; Thornton, I.; Grosjean, M.; Shiffrar, M., editors. *Human body perception from the inside out*. Oxford: Oxford University Press; p. 15-64.

James, W. (1890). *The principles of psychology*. Cambridge: Harvard University Press.

Jeannerod M (2003) The mechanism of self-recognition in humans. *Behavioural Brain Research, 142*, 1-15.

Kammers MP, de Vignemont F, Verhagen L, Dijkerman HC.(2009) The rubber hand illusion in action. *Neuropsychologia. 47*, 204-11.

Kammers MP, Verhagen L, Dijkerman HC, Hogendoorn H, De Vignemont F, Schutter DJ. (2008) Is This Hand for Real? Attenuation of the Rubber Hand Illusion by Transcranial Magnetic Stimulation over the Inferior Parietal Lobule. *Journal of Cognitive Neuroscience*. [Epub ahead of print]

Kanayama N, Sato A, Ohira H. (2008). The role of gamma band oscillations and synchrony on rubber hand illusion and crossmodal integration. *Brain & Cognition 69*, 19-29.

Kanayama N, Sato A, Ohira H.(2007) Crossmodal effect with rubber hand illusion and gamma-band activity. *Psychophysiology. 44*, 392-402.

Karnath,H.O., Baier,B., and Nagele,T. (2005). Awareness of the functioning of one's own limbs mediated by the insular cortex? *J. Neurosci. 25*, 7134-7138.

Keenan, J. P., Rubio, J., Racioppi, C., Johnson, A., & Barnacz, A. (2005). The right hemisphere and the dark side of consciousness. *Cortex, 41*, 695–704

Keysers,C., Wicker,B., Gazzola,V., Anton,J.L., Fogassi,L., and Gallese,V. (2004). A touching sight: SII/PV activation during the observation and experience of touch. *Neuron 42*, 335-346.

Ladavas, E., di Pellegrino, G., Farne, A., & Zeloni, G. (1998). Neuropsychological evidence of an integrated visuotactile representation of peripersonal space in humans. *Journal of Cognitive Neuroscience, 10,* 581–589.

Legrand D & Ruby P (2009). What is self-specific? Theoretical investigation and critical review of neuroimaging results. *Psychological Review, 116*, 252-82.

Lenggenhager B, Tadi T, Metzinger T, Blanke O. (2007)Video ergo sum: manipulating bodily self-consciousness. *Science. 317*, 1096-9.

Lloyd DM.(2007) Spatial limits on referred touch to an alien limb may reflect boundaries of visuo-tactile peripersonal space surrounding the hand. *Brain & Cognition, 64*, 104–9.

Longo M, Schüür F, Kammers MPM, Tsakiris M & Haggard P. (2008) What is Embodiment? A Psychometric Approach. *Cognition, 107*, 978-98.

Longo, M. R., Schüür, F., Kammers, M. P. M., Tsakiris, M., & Haggard, P. (2009) Sense of self alters perceived similarity of hands. *Acta Psychologica* In press

Makin TR, Holmes NP, Zohary E. (2007) Is that near my hand? Multisensory representation of peripersonal space in human intraparietal sulcus. *Journal of Neuroscience, 27*, 731–40.

Makin TR, Holmes NP, Ehrsson HH.(2008) On the other hand: dummy hands and peripersonal space. *Behavioral Brain Research, 191*, 1-10.

Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in Cognitive Sciences, 8,* 79–86.

Maravita A, Spence C, Driver J (2003) Multisensory integration and the body schema: close to hand and within reach. *Current Biology, 13*, R531-R539.

Merleau-Ponty M (1962) *The Phenomenology of Perception* (C Smith, trans.).London, NY : Routledge.

Mitchell, SW. (1866). "The Case of George Dedlow." *The Atlantic Monthly, 18,* 1-11.

Mitchell, SW (1871) . "Phantom Limbs." *Lippincott 's Magazine of Popular Literature and Scienc*e, 8563-9.

Mort DJ, Malhotra P, Mannan SK, Rorden C, Pambakian A, Kennard C, Husain M. (2003). The anatomy of visual neglect. *Brain, 126*, 1986-97.

Morgan, R., Rochat, P. (1997). Intermodal calibration of the body in early infancy. *Ecological Psychology 9,* 1-24.

Moseley GL, Olthof N, Venema A, Don S, Wijers M, Gallace A, Spence C.(2008) Psychologically induced cooling of a specific body part caused by the illusory ownership of an artificial counterpart. *Proceedings of the National Academy of Sciences, 105*, 13169-73

Nightingale S (1982) Somatoparaphrenia: a case report. *Cortex 18*, 463-467.

Pavani, F., Spence, C., & Driver, J. (2000). Visual capture of touch: out-of-the-body experiences with rubber gloves. *Psychological Science, 11*, 353–359.

Pavani F, Zampini M.(2007) The role of hand size in the fake-hand illusion paradigm *Perception, 36,* 1547-54.

Petkova VI, Ehrsson HH.(2008) If I were you: perceptual illusion of body swapping. *PLoS ONE. 3*(12):e3832.

Press C, Heyes C, Haggard P, Eimer M.(2008) Visuotactile learning and body representation: an ERP study with rubber hands and rubber objects. *Journal of Cognitive Neuroscience. 20*, 312-23.

Rochat, P. and Striano, T. (2000) Perceived self in infancy. *Infant Behavior and Development, 23*, 513–530.

Schaefer M, Flor H, Heinze HJ, Rotte M. 2006. Dynamic modulation of the primary somatosensory cortex during seeing and feeling a touched hand. *Neuroimage, 29*, 587-592.

Schaefer M, Heinze HJ, Rotte M. 2005. Seeing the hand being touched modulates the primary somatosensory cortex. *Neuroreport, 16*, 1101-1105.

Schaefer M, Noennig N, Heinze HJ, Rotte M. 2006. Fooling your feelings: artificially induced referred sensations are linked to a modulation of the primary somatosensory cortex. *Neuroimage. 29*, 67-73.

Schwartz,S., Assal,F., Valenza,N., Seghier,M.L., and Vuilleumier,P. (2005). Illusory persistence of touch after right parietal damage: neural correlates of tactile awareness. *Brain, 128*, 277-290.

Schwoebel, J., Coslett, H.B. (2005). Evidence for multiple, distinct representations of the human body. *Journal of Cognitive Neuroscience, 17,* 543-53.

Schütz-Bosbach S, Avenanti A, Aglioti SM, Haggard P.(2009) Don't Do It! Cortical Inhibition and Self-attribution during Action Observation. *Journal of Cognitive Neuroscience. 21*, 1215-27.

Schütz-Bosbach S, Mancini B, Aglioti SM, Haggard P. (2006) Self and other in the human motor system. *Current Biology, 16*, 1830-4.

Schütz-Bosbach S, Tausche P, Weiss C.(2009) Roughness perception during the rubber hand illusion. *Brain & Cognition. 70* 136-44.

Sirigu A, Daprati D, Pradat-Diehl P, Franck N & Jeannerod M (1999). Perception of self-generated movement following left parietal lesion. *Brain, 122* (Pt 10), 1867-1874.

Sirigu A, Grafman J, Bressler K, Sunderland T (1991) Multiple representations contribute to body knowledge processing. Evidence from a case of autotopagnosia. *Brain, 114*,, 629-642.

Shulman, G. L., Astafiev, S. V., McAvoy,M. P., d'Avossa, G., & Corbetta,M. (2007). Right TPJ deactivation during visual search: Functional significance and support for a filter hypothesis. *Cerebral Cortex, 17*, 2625–2633.

Slater M, Perez-Marcos D, Ehrsson HH, Sanchez-Vives MV.(2008). Towards a digital body: the virtual arm illusion. *Frontiers in Human Neuroscience. 2*:6.

Synofzik M, Vosgerau G, Newen A. (2008) I move, therefore I am: a new theoretical framework to investigate agency and ownership. *Consciousness & Cognition, 17*, 411-24

Tsakiris M (2007) The self and its body: functional and neural signatures of body-ownership. In Rossetti Y, Haggard P & Kawato M (eds.) *Sensorimotor foundations of higher cognition, Attention and Performance XXII*. Oxford New York: Oxford University Press

Tsakiris M (2008). Looking for myself: current multisensory input alters self-face recognition. *PLoS ONE 3*(12):e4040

Tsakiris M, Costantini M & Haggard P (2008). The role of the right temporoparietal junction in maintaining a coherent sense of one's body. *Neuropsychologia, 46*, 3014-8.

Tsakiris M, Fotopoulou A. (2008) Is my body the sum of online and offline body-representations? *Consciousness & Cognition, 17*,1317-20; discussion 1321-3

Tsakiris M & Haggard P (2005). The rubber hand illusion revisited: visuotactile integration and self-attribution. *Journal of Experimental Psychology: Human Perception & Performance, 31*,80-91.

Tsakiris M, Haggard P, Franck N, Mainy N & Sirigu A (2005), A specific role for efferent information in self-recognition. *Cognition, 96*, 215-231.

Tsakiris M, Hesse M, Boy C, Haggard P & Fink GR (2007) Neural correlates of body-ownership: a sensory network for bodily self-consciousness, *Cerebral Cortex, 17*, 2235-2244

Tsakiris M, Prabhu G & Haggard P (2006). Having a body versus moving your body: how agency structures body-ownership. *Consciousness & Cognition, 15*, 423-432.

Tsakiris M , Schütz-Bosbach S & Gallagher S (2007) On agency and body-ownership: phenomenological and neurocognitive reflections. *Consciousness & Cognition*, *16*, 645-60

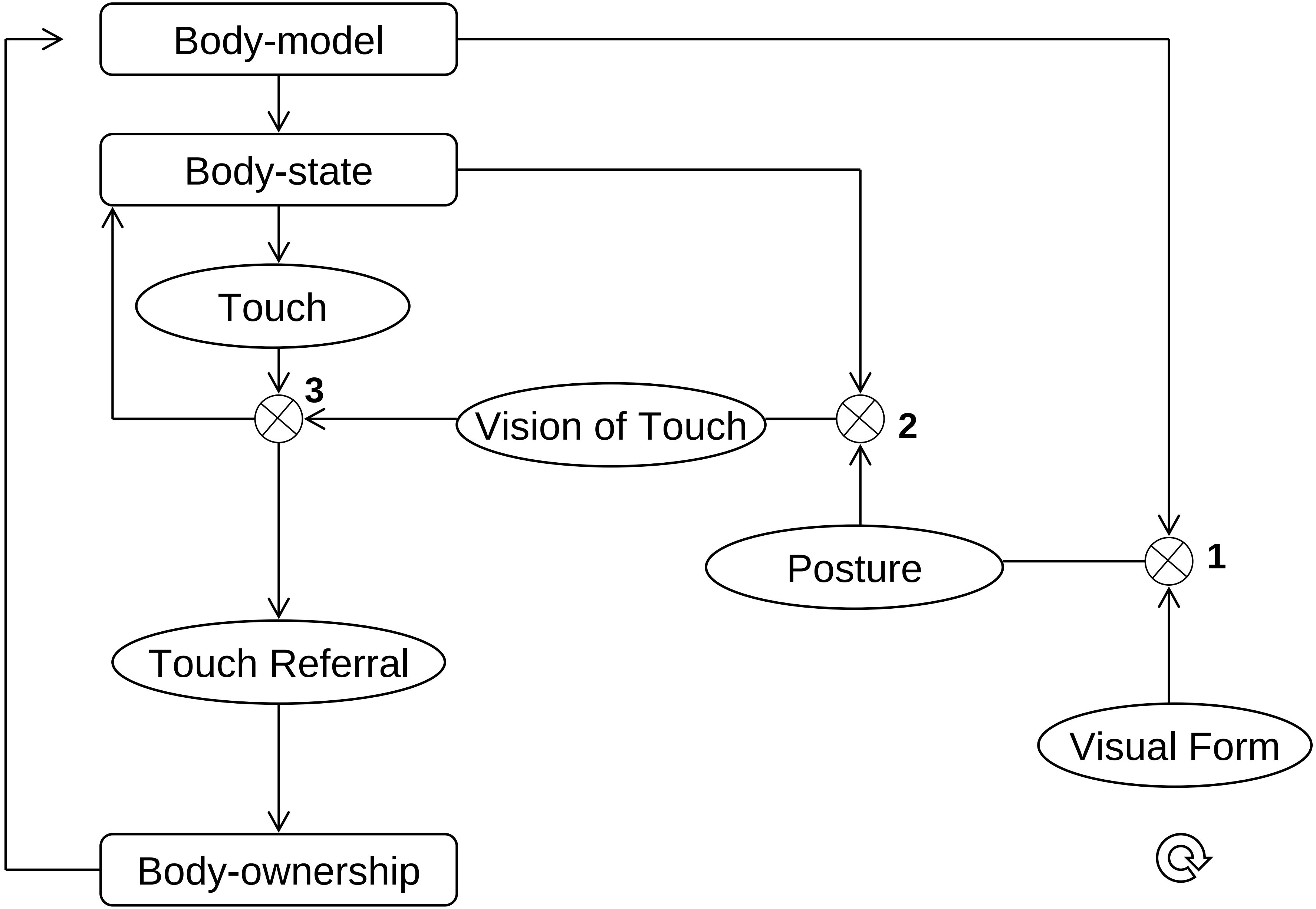
Tsakiris M. Carpenter L & James D. (in press) Hands only illusion: not all objects can be experienced as part of one's body. *Experimental Brain Research*.

Vallar G, Ronchi R. (2009) Somatoparaphrenia: a body delusion. A review of the neuropsychological literature. *Experimental Brain Research*, *192*, 533-51

Van den Bos E & M. Jeannerod (2002). Sense of body and sense of action both contribute to self-recognition. *Cognition*, *85*, 177-187.

Vogeley,K., May,M., Ritzl,A., Falkai,P., Zilles,K., and Fink,G.R. (2004). Neural correlates of first-person perspective as one constituent of human self-consciousness. *Journal of Cognitive Neuroscience. 16*, 817-827.

Waldenfels B (2004) Bodily Experience between Selfhood and Otherness, *Phenomenology & Cognitive Sciences. 3*, 235-248.


Body-model
Body-state
Touch
3
Vision of Touch
2
Posture
1
Touch Referral
Visual Form
Body-ownership