Rubber Hand Illusion Does not Arise from Comparisons with Internal Body Models: A New Multisensory Integration Account of the Sense of Ownership

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Abstract

Human body sense is surprisingly flexible – precisely administered multisensory stimulation may result in the illusion that an external object is part of one's body. There seems to be a general consensus that there are certain top-down constraints on which objects may be incorporated: in particular, to-be-embodied objects should be structurally similar to a visual representation stored in an internal body model for a shift in one's body image to occur. However, empirical evidence contradicts the body model hypothesis: the sense of ownership may be spread over objects strikingly distinct in morphology and structure (e.g., robotic arms or empty space) and direct empirical support for the theory is currently lacking. As an alternative, based on the example of the rubber hand illusion (RHI), I propose a multisensory integration account of how the sense of ownership is induced. In this account, the perception of one's own body is a regular type of multisensory perception and multisensory integration processes are not only necessary but also sufficient for embodiment. In this paper, I propose how RHI can be modeled with the use of Maximum Likelihood Estimation and natural correlation rules. I also discuss how Bayesian Coupling Priors and idiosyncrasies in sensory processing render prior distributions interindividually variable, accounting for large interindividual differences in susceptibility to RHI. Taken together, the proposed model accounts for exceptional malleability of human body perception, fortifies existing bottom-up multisensory integration theories with top-down models of relatedness of sensory cues, and generates testable and disambiguating predictions.

Keywords: rubber hand illusion; multisensory integration; sense of ownership; internal body model hypothesis; Bayesian Coupling Priors

1. Introduction

In the rubber hand illusion (RHI), participants experience a sense of ownership over a fake hand as a result of spatiotemporally congruent stimulation (Botvinick & Cohen, 1998). In a typical study design, the participant's actual hand is hidden from view and a rubber dummy is placed in front of them. After a short period of sustained spatiotemporally congruent stimulation of both hands, e.g., repeated brush strokes, participants start to experience the touch where they see it and, as a consequence, to feel as if the rubber hand was their own. Since its discovery, the RHI phenomenon has become a fruitful experimental paradigm, harnessed in studies on the determinants and constraints of the sense of ownership (Tsakiris & Haggard, 2005; Costantini & Haggard, 2007; Lloyd, 2007; van Stralen et al., 2014; Costantini et al., 2016; Tsakiris, Tajadura-Jimenez, & Costantini, 2011) and sense of agency (Kalckert & Ehrsson, 2012; 2014), both in healthy participants and patients with psychopathological or neuropsychological conditions (Thakkar, Nichols, McIntosh, & Park, 2014; Peled, Pressman, Geva, Modai, 2003; Cascio, Foss-Feig, Burnette, Heacock, & Cosby, 2012; Ding et al., 2017).

Despite intensified research, comprehensive psychological and neurodynamical models of how exactly RHI arises (and in general, of mechanisms that form the basis of embodiment) have not yet been developed, although some attempts have already been made (Tsakiris, 2010; 2017; Apps & Tsakiris, 2014; Ehrsson, 2012; Limanowski & Blankenburg, 2015; Samad, Chung, & Shams, 2015). Although these models underline different processes and constraints for embodiment, there seems to be a general consensus that embodiment results from dynamic interactions between top-down and bottom-up processes (Blanke, Slater, & Serino, 2015; Azañón et al., 2016; Ratcliffe & Newport, 2017; see Samad, Chung, & Shams, 2015, for a bottom-up model). According to the bottom-up approach, the sense of ownership is mainly stimulus-driven and simply results from multisensory stimulation complying with the requirements of the laws of multisensory integration, e.g., spatiotemporal matching of the signals. Originally, RHI was described as a bottom-up phenomenon (Botvinick & Cohen, 1998; Armel & Ramachandran, 2003). However, some studies suggested that certain top-down processes, such as prior knowledge, expectations, pattern recognition, or contextual information, are involved in the process of incorporating external objects (Tsakiris, 2010; Apps & Tsakiris, 2014). In this view, multisensory integration is necessary, but not sufficient, to elicit the illusion, since to-be-incorporated objects have to be highly probable to be taken as part of one's body, for example because of physical resemblance or anatomical plausibility.

The internal body model theory (Tsakiris 2010; Apps & Tsakiris, 2014), stressing the relevance of top-down modulations for multisensory integration processes, is an interesting attempt to provide a neurocognitive explanation of how the subjective sense of ownership arises. Emphasizing the importance of appearance of the to-be-incorporated dummy, it accounts for the attenuation or abolition of RHI for distorted hands (Ratcliffe & Newport, 2017), 2-D hand-like objects (Tsakiris et al., 2009) or non-hand-like objects (Limanowski & Blankenburg, 2016; Tsakiris & Haggard, 2005; Holmes, Snijders, & Spence, 2008; Haans, Ijsselstein, & de Kort, 2008; Guterstam, Gentile, & Ehrsson, 2013); e.g., neither wooden sheets nor blocks can be incorporated. Consistent with the model, the illusion is also absent when a dummy is placed in an anatomically implausible posture (Ehrsson, Spence, & Passingham, 2004; Holle, McLatchie, Maurer, & Ward, 2011). However, "while these observations have been taken to support top-down approaches, they actually do not: dissimilarities between novel object and actual body part are likely to reduce the degree of intersensory matching (the key factor of bottom-up approaches), which renders this factor theoretically nondiagnostic" (Ma & Hommel, 2015a, p.76). In the present article, I will argue that there is no single piece of empirical evidence that unequivocally proves that top-down processes that *do not directly pertain to the properties of stimulation* (such as modulatory top-down influences from an internal body model, prior knowledge of anatomy, or contextual information) are causally relevant for RHI.

As an alternative, I develop a multisensory integration model of RHI[1], which is a substantial extension of the models proposed by Ehrsson (2012), or Samad and colleagues (2015). In this model, RHI arises from the optimal integration of multisensory cues and succumbs to the general laws of multisensory integration, such as the Maximum Likelihood Estimation rule (Ernst & Banks, 2002; Ernst & Bülthoff, 2004) or temporal cross-correlation (Parise & Ernst, 2016). I will also describe the role of the predictive models encoding associations between sensory cues from different modalities (Parise, 2016; van Dam, Parise, & Ernst, 2014; Ernst, 2007). In this view, a reductionist perspective on embodiment emerges – perception of one's own body is taken as a regular form of perception, based on the same principles as perception of external multisensory events (Ma & Hommel, 2015a). I will argue that this model – underlining the need for coherence of stimulation rather than the resemblance of hand and to-be-embodied object – is more parsimonious and comprehensive.

The structure of the paper is as follows. First (section 2), I describe the most influential contemporary models of embodiment, focusing on how they underline the importance of top-down processes; in particular, comparisons with an internal body model. In section 3 I provide a two-pronged argument against the internal body model hypothesis. I appeal to observations from experimental cognitive science that seem to be irreconcilable with this approach and critically

[1] For the sake of clarity, I will focus specifically on the RHI, but the model can be generalized to other related phenomena (e.g., full body illusions) and passively induced sense of ownership in general.

evaluate studies claimed to provide support for this theoretical approach. Then, I proceed to a multisensory integration model, presenting laws of multisensory integration (section 4) and proposing how RHI arises in accordance with these laws (section 5). In the final chapter (section 6), I discuss future challenges and pre-register an experiment that would allow us to disambiguate between multisensory integration and internal body model models.

2. Contemporary Models of the Rubber Hand Illusion

In a neurocognitive model of three critical comparisons, proposed by Tsakiris (2010), multisensory integration processes are preceded by a comparison of visual representation of a to-be-embodied object and a template of a corresponding body-part, stored in an internal body model. The sense of ownership may be spread over objects only if they pass the test of the first critical comparison. Congruence of visual form is crucial at this stage, but some visual features (e.g., skin color) seem to be irrelevant in the first critical comparison. Therefore, the internal body model should not be identified with a body image. In case of a match, a second critical comparison evaluating congruency between seen and felt body postures takes place. The illusion is absent for anatomically implausible positions of rubber dummies or discrepancies in seen and felt hand orientations (Ehrsson, Spence, & Passingham, 2004). However, small discrepancies may be tolerated as long as the stimulation provided is congruent in the hand-centred reference frame (Costantini & Haggard, 2007). Congruent postures lead to recalibration of tactile coordinates to the fake arm (Blanke, Slater, & Serino, 2015), as long as the two hands are not separated by a large distance (<30cm; Lloyd, 2007). The third critical comparison pertains to congruence of visual and tactile information – seen and felt touches. Stimulation that is spatiotemporally congruent in the hand-centred reference frame eventually leads to a subjective sense of ownership.

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The model of three comparisons has recently been made more nuanced within a predictive processing (PP) framework (Apps & Tsakiris, 2014). In the PP approach (Friston, 2005; Clark, 2013), cognitive systems have direct access only to activations in their perceptual subsystems. These sensory signals are sparked by external stimuli (e.g., light hitting the photoreceptors in the retina). To identify the external causes of activations (e.g., objects reflecting the light hitting the receptors), cognitive systems develop and continuously test an internal, hierarchical, and generative model of the world. The model instantiates predictions which flow in a top-down manner, originating from very general and abstract expectations operating at the slower timescales, constrain more detailed predictions on lower levels of the hierarchical model, and determine low-level content operating at the timescale of perception (Seth, Suzuki, & Critchley, 2012). In the face of incongruent sensory evidence, discrepancies are propagated up the hierarchy until they are finally resolved, e.g. via the adjustment of predictions or optimization of higher-level assumptions of the model. “The idea is that a brain operating this way will come to encode (in the form of predictive or generative models) a rich body of information about the sources of signals by which it is regularly perturbed” (Seth, 2014, p. 5), building – through interaction with the environment, in search of dependencies between behavior and perceptual changes – an increasingly comprehensive and accurate model of the world.

Most importantly, the content of perception is constantly negotiated between sensory evidence and predictions based on prior experience, and perception reflects internally generated hypotheses about the causes of the sensory signals. In the case of multisensory experience, the cognitive system must resolve a correspondence problem and determine whether sensory signals from different modalities share a common cause (Welch & Warren, 1980; Ernst & Bülthoff, 2004). To do so, it exploits both spatiotemporal cues – in particular, spatiotemporal correlations of the signals from different modalities (Parise, Spence, & Ernst, 2012) and prior knowledge (van Dam, Parise, & Ernst, 2014). According to Apps and Tsakiris (2014), RHI occurs when the probability that a rubber hand is one's own hand exceeds the probability of one's own hand being one's own. Note that the former is equivalent in meaning to a situation in which a common cause is ascribed to multisensory signals. Given that discrepancies between seen and felt touches are substantial, the solution to a correspondence problem largely depends on the prior probability. It is determined by the visual form of the to-be-embodied object and its orientation in space (both of which may be grouped under the term "body-related visual information"; Blanke, Slater, & Serino, 2015). This body-related visual information is of particular importance in this context, since the cognitive system ascribes higher reliability to visual rather than tactile or proprioceptive signals, based on the history of their lower variability (Hohwy, 2012; Limanowski & Blankenburg, 2016). Therefore, for body-related visual information matching predictions generated under the hypothesis "that is my hand", a subjective sense of ownership occurs (Apps & Tsakiris, 2014). The PP based model has been recently refined by Tsakiris (2017) who stresses the importance of interoception for body ownership in the self-other context.

3. The Internal Body Model Hypothesis Does Not Fit with the Empirical Evidence

It is difficult to specify what kind of empirical data could directly support or count against the internal body model hypothesis, as precise scientifically tractable predictions and falsifiability conditions are rarely specified by its proponents. However, some phenomena that seem to be irreconcilable with internal body model hypotheses can be identified. In this section, I will discuss studies that show that non-hand-like objects and virtual effectors can actually be incorporated and the illusion is not attenuated as compared to hand-shaped objects or virtual hand-like effectors (3.1). In the next subsection, I will summarize the reports showing that the use of differently morphed objects or hands placed in anatomically implausible postures necessarily entails elevated sensory mismatch and, as such, cannot support the internal body model hypothesis (3.2; see also Ma & Hommel, 2015a). Finally (3.3), I will critically evaluate the alleged neuroscientific support for the model. In particular, I will show that neuroscientists succumb to a consistency fallacy (Mole & Klein, 2010; Coltheart, 2013) when discussing results in favor of the internal body model hypothesis (e.g. Limanowski & Blankenburg, 2015; Zeller, Friston, & Classen, 2016).

Importantly, the critique will be based on the studies employing both active (embodiment as a result of active exploration with a coherent sensory feedback) and passive (embodiment as a result of passively received spatiotemporally congruent stimulation) elicitation paradigms. The complex interplay between senses of ownership and agency has been a subject of long and intense debate (Tsakiris, Schütz-Bosbach, & Gallagher, 2007; Tsakiris, Longo, & Haggard, 2010; Kalckert & Ehrsson, 2012; 2014; Tsakiris, Prabhu, & Haggard, 2006). Kalckert and Ehrsson (2012), employing an RHI paradigm, provided evidence for double dissociation between the sense of ownership (exclusively present for passive movements) and agency (sustained for incongruently positioned hands). These results are in line with neuroscientific evidence showing that separate neural substrates underlie experiences of ownership and agency (Tsakiris, Longo, & Haggard, 2010). On the other hand, 'self-recognition, in the sense of correctly recognizing a visual object or event as "me" or "mine" seems to depend largely on efference and agency' (Tsakiris, Schütz-Bosbach, & Gallagher, 2007, p. 655). Visuomotor elicitation is one of the established methods of induction of the sense of ownership and, according to some, "agency is a much stronger modus for inducing embodiment than multi-sensory stimulations" (Aymerich-Franch & Ganesh, 2016, p. 34), although data does not necessarily support such strong claims:

visuomotor stimulation results in illusion strengths spanning below maximal ratings (Sanchez-Vives, Spanlang, Frisoli, Bergamasco, & Slater, 2010, tab. 2; Dummer, Picod-Annand, Neal, & Moore, 2009, tab. 2) that do not significantly differ from passive induction methods (Kalckert & Ehrsson, 2014; Dummer, Picod-Annand, Neal, & Moore, 2009).

Taken together, senses of ownership and agency, although certainly independent to a certain extent, seem difficult to disentangle. In an important study on the multidimensionality of RHI experience (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008), questionnaire items such as "…it seemed like I could have moved the rubber hand if I had wanted" or "…it seemed like I was in control of the rubber hand." were actually included in an "embodiment" factor. Tsakiris (2010, p. 703), when presenting the internal body model hypothesis, openly brackets out reciprocal interactions between the sense of ownership and agency, and focuses on the sense of ownership per se. Therefore, I assume that critical comparison with a stored visual representation should be a prerequisite for any sense of ownership, regardless of the induction method and degree of the associated feeling of agency.

3.1. Objects that do not match the representation stored in the internal body model can actually be incorporated

Ma & Hommel (2015a) have shown that the sense of ownership may be spread over virtual 2D shapes – balloons and rectangles. In their experiments, using mediated-reality conditions, they displayed a virtual effector on a monitor. The participants were asked to freely perform two kinds of movements: opening/closing of the hand and changing its orientation. The virtual effector changed in shape or color in synchrony with the participants' movements, e.g., opening one's hand made it bigger or greener. As a result, participants reported a sense of ownership over a disconnected (separated by a distance) and anatomically implausibly placed (the screen was oriented perpendicularly to the floor and the participant's hand) virtual balloon (exp. 1); the strength of the illusion increased after a virtual rectangle was displayed horizontally on a monitor placed closer to the participant's body and with a textile covering the space between the participant and the monitor (exp. 2). The strength of the illusion did not differ for virtual rectangles and hands. In their follow-up study, Ma and Hommel (2015b) showed that the active exploration of a mediated-reality environment coupled with sensory feedback on a virtual effector induces a sense of ownership both over rectangles and hands and, even though the illusion was stronger for the hand-resembling effector, the visual form did not interact with the synchronicity of stimulation. This finding contradicts the model proposed by Tsakiris (2010), as it suggests that visual resemblance did not further influence multisensory integration processes (the illusion was reported to be stronger for hand-like objects both in synchronous and asynchronous conditions).

On the basis of their findings, Ma and Hommel (2015a; 2015b) propose that connectedness, spatial proximity, and multimodal correlations are crucial for the sense of ownership to arise. Active exploration of an environment significantly increases the amount of sensory information revealing multisensory contingencies and thus strengthening the sense of ownership. Appearance seems to be irrelevant; the very possibility of embodying a 2D effector is in direct contradiction with the model of critical comparisons (Tsakiris, 2010), as the visual form of this shape would have been extremely unlikely to pass a test-for-fit stage. It is also worth noting that the possibility of incorporation of a detached and perpendicularly presented 2D virtual effector – even if the strength of the sense of ownership induced was relatively weak – also brings into question the importance of anatomical plausibility.

An even more striking phenomenon – the "invisible hand illusion" (Guterstam, Gentile, & Ehrsson, 2013) – arises when congruent spatiotemporal patterns of stimulation are delivered to a participant's real hand and an empty space. As a result, tactile sensations are referred to a volume of empty space and a sense of ownership is induced. Since visual information pertaining to structural properties or anatomical plausibility is lacking, the occurrence of this phenomenon seems to question the importance of body-related visual information (or to-be-embodied-object-related visual information) – it is neither a necessary factor (Tsakiris, 2010) nor a constraint (Blanke, Slater, & Serino, 2015) for a sense of ownership to manifest. However, this does not mean that visual information is irrelevant in general, but rather that it is visual information pertaining to spatiotemporal properties of stimulation that matters, as the invisible hand illusion arises only when 1) seen and felt brushstroke trajectories are carefully matched in 3-d space (note that during the experiment, "a trained experimenter moved the paintbrush […] following the shape of the knuckles and angles of the finger phalanges, as if it were touching an identical invisible right hand", p. 1080) and 2) "stimulation" of an empty space is confined to peripersonal space (PPS). Taken together, these results seem to be irreconcilable with the internal body model hypothesis without additional assumptions (e.g., that participants were imagining the real hand in an empty space, which is impossible when the space is occupied by a dissimilar object; Aymerich-Franch & Ganesh, 2016).

Aymerich-Franch and colleagues (2017a), utilizing a virtual reality set-up, showed that sense of ownership may be spread over robotic arms dissimilar to human hands in terms of anatomical properties: lacking fingers (exp.1) or with a metal gripper at the end (exp. 2). In the experiment, the participant's perspective was shifted to a human-sized robot's point of view with the use of a head-mounted display receiving visual feedback from the camera mounted on the robot's head. After careful matching of the positions of the robotic and real arms, synchronous visuotactile stimulation was delivered to both hands. A sense of ownership was successfully induced for both robotic arms and did not differ in strength from real-hand conditions. Importantly, stimulation was delivered to the knuckle area. In their other work, using a very similar virtual-reality setup along with a robotic arm identical to the one used in exp. 1 of the experiment discussed above, Aymerich-Franch and colleagues (2017b) demonstrated that around 60% of participants experienced a haptic sensation when they observed – from the first person perspective – the robot touching a curtain, without any tactile feedback. The sensation felt was projected to the area around the knuckles, which "might indicate that participants identified the end of the robot hand with the area corresponding to the knuckles" (2017b, p. 224). Therefore, it seems that the tactile stimulation was delivered to the corresponding parts of real and robotic hands, resulting in a spatiotemporally congruent stimulation. Taken together, this "study demonstrates that humans can embody robotic limbs which are drastically different from a human limb in terms of shape, color, material, and texture" (Aymerich-Franch, Petit, Ganesh, & Kheddar, 2017a, p. 488).

Tsakiris (2010) directly states that "body-model should not be equated with conscious body image" (p. 707) and points to the fact that some body/hand features are irrelevant in the context of first critical comparison. However, features like 1) hand-like shape, 2) tridimensionality 3) solid state and occupation of a certain space, 4) finger possession, and 5) skin-like external layer seem to be too fundamental to be excluded – if they are irrelevant, which features actually do matter? Note that other properties, such as hand color, size of the hand and its fingers, quantity of limbs, and hand gender should also be excluded from the putative internal body model – all of them have been shown experimentally to be irrelevant to the illusion: hands of different skin color (Holmes, Snijders, & Spence, 2006; Farmer, Tajadura-Jiménez, & Tsakiris, 2012), elongated arms (Kilteni, Normand, Sanchez-Vives, & Slater, 2012), large hands (Pavani & Zampini, 2007), shrunken and elongated fingers (Perera, Newport and McKenzie, 2015), supernumerary limbs (Ehrsson, 2009; Guterstam, Petkova, & Ehrsson, 2011; Chen, Huang, Lee, & Liang, 2018), and hands of the opposite gender (own unpublished observations) may be incorporated.[2] Most of these findings are generalizable to a global body level, as shown by experiments in body-swap and virtual reality paradigms (see Aymerich-Franch & Ganesh, 2016, for a review). Thus, top-down constraints stemming from an internal body model would have to evince an enormous plasticity and interindividually variable selectivity of relevant features. It is redundant to posit an explanatory mechanism of critical comparison between visual representation and the appearance of the to-be-embodied object, given that most fundamental body features do not enter the comparison and not a single visual body property has been unambiguously identified as doing so. Therefore, we should assume that converging empirical evidence unequivocally contradicts the internal body model hypothesis.

Moreover, this unidentified set of relevant features should prompt us to question the function of such internal body models. According to Tsakiris (2010), the filter operates in a gradual rather than a bottleneck fashion: “the more the viewed object matches the structural appearance of the body-part’s form, the stronger the experience of body-ownership will be” (p. 707). Consistently, a gradual reduction in the strength of the feeling of ownership is sometimes reported with the distortions of the appearance of the hand (e.g., Ratcliffe & Newport, 2017).

[2] Note that the predictive processing framework may predict the exclusion of some body properties from the body model; a continuously adapting and liberal model would be more functional in the case of constantly changing body properties (e.g., hand size changes when one puts on weight, skin color temporarily changes from bruises and sun exposition, etc). However, this applies only to a limited set of properties.

However, the role of the critical filter would be even more mysterious if its function were not to let an object representation through. What would be the function of gradually operating and extremely liberal body models composed of sets of interindividually variable properties, which are competitive and functionally distinct from other body representations, e.g., body image and body schema, given the scarcity of everyday applications for such models?

3.2. Experimental results supporting internal body model hypothesis are actually inconclusive

Some objects have been repeatedly shown to resist embodiment: particularly wooden blocks (Guterstam, Gentile, & Ehrsson, 2013), sticks (Tsakiris & Haggard, 2005), and sheets (Tsakiris et al., 2009); this effect is driven by inconsistent shape rather than the texture of the surface (Haans, Ijsselstein, & de Kort, 2008; Aymerich-Franch, Petit, Ganesh, & Kheddar, 2017a). Since these objects do not resemble real hands, such reports are cited as supporting "interaction of top-down and bottom-up processes" hypotheses in numerous recent empirical and theoretical contributions (Ratcliffe & Newport, 2017; Tsakiris, 2017; Azañón et al., 2016). In this line of reasoning, visual representations of these objects are rejected during the first critical comparison (Tsakiris, 2010); therefore, one can say that top-down knowledge of the appearance of one's hand precludes embodiment.

However, these reports cannot account specifically for the internal body model hypothesis since they do not distinguish between the effects of distorted appearance and reduced intersensory matching and, as such, are actually inconclusive (Ma & Hommel, 2015a). As opposed to the studies carried out by Guterstam and colleagues (2013) or Aymerich-Franch and colleagues (2017a), stimulation delivered to the object did not closely mimic the one delivered on participant's hand; in particular, stimulations were incongruent in tridimensional space. In

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most of the studies, control objects were flat (e.g. Gutestam, Gentile, & Ehrsson, 2013; Tsakiris et al., 2009; Haans, Ijsselstein, & de Kort, 2008). As a result, stimulation delivered to objects was ideally parallel to the underlying surface, whereas stimulation delivered to hands was more or less diagonal. This could be crucial in the context of multisensory integration processes, since the rubber hand illusion is very sensitive to discrepancies in stimulation orientations in the hand-centred reference frame (Costantini & Haggard, 2007; Gutestam, Gentile, & Ehrsson, 2013).

In some cases, there are actually good reasons to ascribe the absence of the illusion to elevated sensory mismatch rather than to distorted appearance. For example, Tsakiris, Carpenter, James, and Fotopoulou (2009) employed five different objects: a wooden sheet (object 1) that was gradually transformed to a flat hand-like shape with all fingers (object 4) via the addition of a thumb-like feature (object 2) and wrist (object 3). A 3D real-sized prosthetic hand was the fifth object. Despite gradual likening to the hand, the illusion was absent for all flat objects (objects 1-4) and could only be elicited for a realistic prosthetic hand. These results seem to contradict the internal body model hypothesis as presented by Tsakiris (2010, p. 707): “the more the viewed object matches the structural appearance of the body-part’s form, the stronger the experience of body-ownership will be”. It seems that increased intersensory matching present in the fifth condition was an actual turning point (note that intersensory matching was increased in other sensory domains as well, e.g., the expected weight of the prosthetic hand is consistent with the felt weight of one’s hand as opposed to thin wooden sheets). Surprisingly, the authors interpret their results as coherent with the internal body model hypothesis: “the viewed object must fit with a reference model of the body that contains important structural information about body parts” (Tsakiris, Carpenter, James, & Fotopoulou, 2009, p. 343).

3.3 There is no direct neuroscientific evidence for the internal body model hypothesis

Apps and Tsakiris (2014) list a set of brain areas engaged in self-attribution processes. Distinct functional properties are ascribed to each of the structures, with “temporoparietal junction (TPJ) processing the confluence of visual information and bodily related information, the anterior insula (AI) processing the confluence of emotional, interoceptive and motor information about the body, the intraparietal sulcus (IPS) processing visuo-spatial information about somatosensory input to the body and the inferior frontal gyrus processing the mappings between abstract rules and the body (IFG)” (Apps & Tsakiris, 2014, p. 94). These structures have been repeatedly shown to be activated during the rubber hand illusion (Limanowski & Blankenburg, 2014). The role of the anterior insula should perhaps also be emphasized (Tsakiris, 2017). A meta-analysis conducted by Grivaz, Blanke, and Serino (2017) has shown that the anterior insula is selectively activated during body ownership, but not when multisensory cues are simply presented within peripersonal space. Moreover, the right insular cortex lesion prevents the integration of body-related exteroceptive and interoceptive signals into the united self in cardio-visual stimulation conditions (Ronchi et al., 2015), which occurs in healthy individuals (Aspell et al., 2013; Suzuki et al., 2013). However, neuronal evidence for the internal body model is mainly circumstantial.

The strongest neuroscientific evidence for the internal body model hypothesis comes from the study carried out by Limanowski and Blankenburg (2015), who proposed a neurodynamic PP-based model. Using dynamic causal modeling (Friston, Harrison, & Penny, 2003), they showed the strengthening of effective connectivity from lower-level perceptual areas, such as the lateral occipital cortex (LOC) and the secondary somatosensory cortex (SII), to the higher-level integrative multisensory hub (intraparietal sulcus; IPS) during spatially congruent stimulation (as opposed to incongruent stimulation). This bottom-up model outperformed bidirectional and top-down models. Counterintuitively, the bottom-up model was interpreted as lending empirical support to a PP-based interpretation. According to the authors, spatiotemporal congruence of seen and felt touches leads to their association and ascription of a common cause. Due to a discrepancy in the locations of seen and felt touches, there is an increased prediction error propagated up the hierarchy from LOC to IPS which counters this mismatch via recalibration of somatosensory reference frame coordinates onto the visual reference frame. This leads to an error suppression in LOC, but elevates the prediction error in somatosensory areas since the changed somatosensory coordinates do not match skin-based and proprioceptive information about the location of the hand.

This line of reasoning is highly speculative. Firstly, such interpretation rests on the assumption that enhanced neuronal activity reflects the spreading prediction error. Secondly, one would expect effective top-down modulations to come forward, since, according to the PP model presented by Apps and Tsakiris (2014, p. 89), “surprise in one system can be minimised by the top-down effects of multisensory nodes”. In particular, modulations from IPS to LOC silencing prediction errors via recalibration of the somatosensory reference frame should be present in spatially congruent stimulation (and, perhaps, error-related effective connectivity from LOC to IPS should not be present as these errors would have to be resolved for the illusion to arise). However, enhanced connections from IPS to LOC were found independently of congruency and were interpreted as top-down attention to visual processing resulting in increased weighting of visual signals in multisensory integration processes. Then again, this interpretation may be challenged. Intrinsic connectivity in both LOC and SII was attenuated regardless of the experimental context (fig. 6, p. 2297). Lowered intrinsic connectivity in the primary somatosensory cortex during RHI was also found – using dynamic causal modeling – and interpreted by Zeller, Friston, and Classen (2016) as reduced precision weighting. If this is true, reduced intrinsic connectivity could not result from top-down attention in the PP framework. Moreover, Limanowski and Blankenburg (2015) refer to the finding that, during performance of a visuotactile task, connection weights between LOC/SII and IPS change in accordance with the reliability of the corresponding modality (e.g., for reliable visual information, the connectivity between LOC and IPS is enhanced; Beauchamp, Pasalar, & Ro, 2010). However, Beauchamp and colleagues (2010) are agnostic about the causal direction (and they seem to think of it as of a bottom-up rather than top-down connection; e.g. see description of fig. 5). They also explicitly write that their "data is incompatible with a simple effect of top-down visual attention, and consistent with behavioral studies showing that reliability weighting is independent of attention" (p. 8).

Interestingly, Limanowski and Blankenburg (2015) focus on the PP-based explanation, which they very thoroughly analyze, despite their own claim that these effects "may also be interpreted as reflecting processes of multisensory integration that produce the coherent ownership experience" (p. 2301). In this simpler interpretation, signals from LOC and SII would evoke multisensory integration processes in IPS only in the case of congruent information. However, this path has not been explored and the latter explanation was dismissed as being consistent with the PP account as well. Thereby, Limanowski and Blankenburg commit a consistency fallacy (Cole & Klein, 2010; Coltheart, 2013) – they claim that their "results comply with the idea that the brain's inference mechanisms rely on the hierarchical propagation of prediction error" (p. 2284) even though these results are not inconsistent with a competing theory. As such, the study is theoretically nondiagnostic since the results do not specifically account for any theory. That said, the study is cited in contemporary literature as providing *empirical support* for the internal body model hypothesis (Tsakiris, 2017; author's emphasis).

Finally, Limanowski and Blankenburg (2015), employing dynamic causal modeling, did not define models that would count against PP theory. Instead, they elaborated a PP-based post-hoc explanation – and the plausibility of such explanations may depend on rhetorical capabilities rather than data. Falsifiability conditions should be pre-defined prior to the experiment – since the authors did not argue what kind of data would be incompatible with the theory, obtaining such data was impossible. According to Coltheart (2013), this is a form of consistency fallacy, since the experiment is planned in such a way that it cannot provide results inconsistent with the theory being tested. This criticism may also apply to other PP-inspired studies employing dynamic causal modeling to study how RHI arises (e.g. Zeller, Friston, & Classen, 2016).

4. Multisensory Integration

According to Ehrsson (2012, p. 797), "the natural constraints of the rubber hand illusion fit nicely with the multisensory integration hypothesis". It is constrained by peripersonal space (Lloyd, 2007) and arises only when synchronous stimulation is applied to both hands (Botvinick & Cohen, 1998); therefore, it obeys the basic rules of multisensory integration, which say that stimuli originating from similar spatial locations and presented at the same time are more strongly integrated (Holmes & Spence, 2005). Stimulation patterns misaligned in the hand-centred reference frame, even when aligned in external space, result in a reduction in the strength of the illusion (Costantini & Haggard, 2007). RHI also disappears when there is extreme anatomical implausibility in the dummy's position (e.g., when it is rotated by 90°; Tsakiris & Haggard, 2005; however, incompatible body postures may be taken as a top-down factor when interpreted as a body-related visual information; e.g., Blanke, Slater, & Serino, 2015; Apps &

Tsakiris, 2014), which underlines the importance of visuoproprioceptive coherence (Erro, Marotta, Tinazzi, Frera, & Fiorio, 2018; however, small discrepancies in hand orientations may be tolerated; Costantini & Haggard, 2007).

In the present paper, multisensory integration theory, as compared to the one presented by Ehrsson (2012), will be extensively developed: RHI actually follows much more complex multisensory integration rules – e.g., reliance on the correlation of temporal structures rather than mere temporal coincidence (van Dam, Parise, & Ernst, 2014; Parise, Harrar, Ernst, & Spence, 2013), the optimal integration rule (Ernst & Bülthoff, 2004), and crossmodal correspondences (Parise, 2016). As such, it may be modeled as a multisensory integration process (Samad, Chung, & Shams, 2015). In particular, I propose that RHI does not involve any dedicated neurocognitive mechanism of self-recognition or embodiment. In this reductionist view, RHI occurs when seen and felt touches are falsely interpreted as being caused by the same external event. Since tactile modality defines real-time boundaries of the body (informing about current body-world touchpoints), any ascription of the common cause to visuotactile signals necessarily results in recognition of an object as one's body part – and it may be an external object in the case of actually distinct origins of spatiotemporally synchronized patterns of seen and felt touches. This approach is similar to the one presented by Samad and colleagues (2015) who proposed an elegant Bayesian computational model of RHI. Important differences between the models will be discussed in sections 5.2 and 6.1.

4.1. Maximum Likelihood Estimation

The basic concepts of multisensory integration theory should be introduced before the presentation of the developed multisensory integration model of RHI. None of the sensory modalities can provide reliable information about the multidimensional structure of the world in all circumstances (Ernst & Bülthoff, 2004). Unimodal sensory estimates may be 1) noisy, due to changing environmental conditions and spontaneous neural activity, 2) specialized – signal reliabilities vary depending on the nature of the perceptual task. For example, visual modality is appropriate for the localization task because of its high spatial resolution. Nonetheless, auditory modality tends to dominate over vision in temporal judgments (Shams et al., 2000; Burr, Banks, & Morrone, 2009) because of the higher sampling rate of auditory signals, 3) biased – unimodal estimates may be invariant yet repetitively inaccurate, and 4) ambiguous. Multisensory integration of unimodal signals can alleviate these problems (van Dam, Parise, & Ernst, 2014). Sensory information is integrated according to the Maximum Likelihood Estimation (MLE) rule (Ernst & Bülthoff, 2004). Given that consecutive sensory samples yield slightly varying estimates, environmental properties may be represented as likelihood functions with varying degrees of uncertainty (width of the distribution). On this basis, assuming that noises in different modalities are normally distributed and independent from each other, the reliability of each signal may be quantified as its inverse variance. Then, weights inversely proportional to a signal's variance are ascribed to each of the signals, yielding the optimal estimate – a weighted average of unimodal estimates.

Note that, in contrast with the concept of precision weighting in PP (Hohwy, 2012), ascription of weights may take place in a bottom-up fashion – based on the signal's variance in a short time bracket directly preceding the estimate (quasi bottom-up; Ernst & Bülthoff, 2004) or the size of receptive fields of neurons providing the estimate (Parise & Ernst, 2016). In the latter, the "reliability of a signal's estimate is the emergent property of neuronal tuning of the particular stimulus" (Parise & Ernst, 2016, p. 6) and is inversely proportional to the size of receptive fields of activated neurons. Let's take V1 neurons as an example – they are highly specialized (e.g., react only to particular, well-defined orientations) and have small receptive fields. Therefore, their activations are highly specific. In the case of activations of neurons sensitive to a particular orientation and the concurrent lack of or weak activation of neurons with overlapping receptive fields, but sensitive to other orientations, the distribution of responses has a well-defined peak (Ernst & Banks, 2002) and the signal is highly precise.

The optimal integration model has substantial empirical support and many perceptual phenomena may be modeled in this way (van Dam, Parise, & Ernst, 2014). Alais and Burr (2002) have shown that “visual capture” in an audiovisual spatial localization task (present in the well-known “ventriloquist effect”) may be reversed after adding noise to a visual signal. Even more importantly, in the context of this paper, Ernst and Banks (2002) obtained analogous results for a visuo-haptic task in which participants had to determine which of two consecutively presented ridges is taller. For unimodal discriminations, vision proved to be more reliable than touch when either no or small (67%) noise was added, equally reliable for moderate noise (133%), and less reliable for intense noise (200%). Using unimodal data, an MLE-based model was developed to predict weights ascribed to particular modalities in a crossmodal task in which visual and tactile signals were slightly discrepant for the second ridge. Height judgments followed the MLE rule: they relied on visual signals for low noise conditions and on tactile signals when high noise was added to a visual signal; thus, weights were inversely proportional to the signals’ variances. Van Dam, Parise, and Ernst (2014) provide a comprehensive review of a wide variety of crossmodal and within-modality effects that have been experimentally shown to obey the Maximum Likelihood Integration rule.

4.2. The Correspondence Problem and probabilistic models of multisensory integration

Multisensory integration improves the precision of estimates of a given property of interest as compared to unimodal estimates (van Dam, Parise, & Ernst, 2014) and may improve them even if the weights ascribed to particular signals are suboptimal (Ernst & Bülthoff, 2004). However, its benefits are seen only if integrated signals are actually caused by the same external event – otherwise, there is a risk that an inaccurate combined estimate biased by irrelevant information will be found. Therefore, the cognitive system has to solve the so-called correspondence problem and determine whether various signals have the same underlying external cause. To perform this task, perceptual systems use various sources of information, e.g., pertaining to the spatiotemporal proximity of signals (the closer in space and time they occur, the more likely they are to share a common cause; Holmes & Spence, 2005) and temporal cross-correlation (van Dam, Parise, & Ernst, 2014; Parise & Ernst, 2016). The latter seems to be more important than mere temporal coincidence; unimodal signals are integrated if they co-vary across time and have closely correlated complex temporal structures (Parise, Harrar, Ernst, & Spence 2013; Parise, Spence, & Ernst, 2012).

In addition to the bottom-up factors discussed above, cognitive systems use knowledge of natural mappings between sensory cues from different modalities – crossmodal correspondences – as a top-down factor determining whether sensory fusion will take place. Parise (2016) discusses three categories of cue pairings: redundant cues (both modalities provide information about the same environmental property – e.g., the stimulus location), related cues (when cues from different modalities pertain to seemingly non-related sensory features, but are reciprocally predictable to a certain extent, e.g., the auditory pitch and the object's size) and unrelated cues. Cues may be associated on the basis of statistical intersensory dependencies found in the process of the continuous interaction with the environment. For example, high sensory pitch and small size may be associated since they frequently co-occur. In this manner, “sensory systems become fine-tuned to the natural mapping across cues” (Parise, 2016, p. 13), developing predictive models that encode which signals tend to go together and how strongly they are related. These predictive models seem to be very flexible and experience-informed. Studies implementing perceptual learning paradigms show that new crossmodal mappings may be learned in laboratory conditions for initially unrelated sensory cues (Ernst, 2007) and existing intersensory associations may be reversed after repeated exposure to inverted mapping between cues (Flanagan, Bittner, & Johansson, 2008).

Within a Bayesian framework, the input of these predictive models may be operationalized as Bayesian coupling priors representing beliefs that two signals were caused by the same external event (van Dam, Parise, & Ernst, 2014). The distribution of a coupling prior is determined both by spatiotemporal properties of signals (spatiotemporal proximity, correlation of a temporal structure) and their learned relatedness. Unimodal estimates are multiplied by a coupling prior to determine whether a combined estimate or separate estimates are more likely to reflect external cause(s) of the sensory signals. When particular sensory cues are considered to be independent, the distribution of a coupling prior is flat (with infinite variance and no clear peak) and posterior is determined by separate unimodal estimates. For narrow distributions with well-defined peaks and minimal variance, indicating stronger association between the senses, sensory fusion takes place and the combined estimate is provided – since redundant cues follow a one-to-one mapping, the entire variance of one of the unimodal estimates may be explained by its relation to another (hence their “redundancy”). Importantly, for slight intermodal discrepancies and partial relatedness, “partial fusion will take place, and there will be perceptual benefit for estimating the property of interest” (van Dam, Parise, & Ernst, 2014, p. 219).

Therefore, multisensory integration should be envisioned as a gradually operating process, rather than a "go/no-go" process.

5. Multisensory Integration Hypothesis

Equipped with the concepts of the multisensory integration theory, in this section, we will develop a parsimonious and comprehensive model of RHI. The proposed model pertains to passively-induced RHI (its implications for visuomotor variants of induction of the sense of ownership are discussed in section 6.2).

5.1. Multisensory cues relevant for RHI

During the multisensory stimulation which induces RHI, the cognitive system observes simultaneous visual and tactile signals that originate in PPS and are spatially congruent in the hand-centred reference frame, yet discrepant in external space. These are redundant cues: 1) they pertain to the same environmental property (the area of space from where tactile sensations emerge), 2) as such, they have been learned to go together reliably: in everyday interactions, spatiotemporally congruent visuotactile signals unambiguously attest that a particular spot on one's body is being touched and, 3) the temporal structure of brushstrokes is complex and highly correlated (note that RHI is stronger for irregular than for regular synchronized stimulation patterns; Guterstam, Petkova, & Ehrsson, 2013). As a result, Bayesian coupling priors have a distribution with a well-defined peak, promoting sensory fusion of visual and tactile signals. The common cause of both signals is ascribed and the touch is now referred to a rubber dummy (the only one object touched in one's visual field). Since tactile modality defines body boundaries, the sense of ownership is spread over a rubber hand.

In the proposed model, coupling prior distributions dispense with the need for internal body models (Tsakiris, 2010, 2017; Apps & Tsakiris, 2014), as the relevant visual information is stimulation-related rather than body- or object-related. To-be-embodied objects are reconceived of as "carriers of sensory signals"; any properties that are irrelevant in the context of the stimulation (e.g. hand color, general appearance, or hand-like character) remain irrelevant for embodiment as well. It is the congruency of visual and tactile signals that steepens the distribution of a coupling prior, promoting sensory fusion and the occurrence of the illusion. In particular, visual and tactile signals following parallel spatial curvatures in tridimensional space (even in the absence of the object; Guterstam, Gentile, & Ehrsson, 2013) and the hand-centred reference frame (Costantini & Haggard, 2007), as well as complex, irregular temporal patterns (Guterstam, Petkova, & Ehrsson, 2011) lend weight to the hypothesis that there is a single external cause underlying distinct unimodal estimates. When stimulation patterns diverge (e.g., brushstrokes are delivered perpendicularly to the underlying surface on a block of wood and diagonally on the hand), the coupling prior flattens, since these signals are very unlikely to go together. RHI sensitivity to postural incongruences also underlines the importance of visuoproprioceptive coherence; however, the full list of relevant sensory cues is yet to be elaborated. Other factors, such as 1) contact area between the underlying surface and the dummy, 2) the dummy's expected weight, and 3) the inclination and positioning of the participant's fingers may play an important role (these factors may be challenging to control in experiments, given the large individual differences in weight, size, skin conformity or finger shape, and positioning among the participants).

Analogously, if the everyday sense of ownership is driven by multisensory integration processes, disownership of a real hand should occur as a result of the breakdown of integration of visual, tactile, and proprioceptive signals. This has been shown by Newport and Gilpin (2011) who described a "disappearing hand trick" exemplifying the relevance of multisensory congruence for the sense of ownership over one's own limb. In their experiment, they used mediated-reality conditions so the participant could view a live video stream of their own hand. Initially, the displayed and real locations overlapped. Then, the real hand was displaced using the sensorimotor adaptation procedure – participants had to keep the hand within the boundaries of the display. Since the displayed area was very slowly shifting to one side, participants were subliminally displacing their own hands in accordance with the direction of the shift. After the sensorimotor adaptation procedure, the displaced hand could not be found with the contralateral hand reaching to the perceived location of the real hand. This resulted in an immediate loss of ownership over the displaced hand, manifesting as an inability to assess the real position of the hand, self-reported disownership, and lack of physiological arousal in a situation threatening to the hand in both perceived and real locations. In the authors' words (p. 805), "the lack of hand awareness (and associated lack of a skin conductance response) in the disappearing hand condition indicates a failure to resolve disintegrated vision (removed), proprioception (realigned) and touch (absent) in these key neural networks, resulting in a lack of ownership for the real hand". Recently, it has been shown that a breakdown of synchronicity of visuotactile feedback in mediated reality conditions results in disownership over the real hand (Kannape, Smith, Moseley, Roy, & Lenggenhager; 2018)

Moreover, the multisensory integration model predicts interindividual differences in the distribution of coupling priors, accounting for interindividual differences in proneness to the illusion. In particular, it operationalizes these differences as resulting from idiosyncrasies in perceptual processing rather than liberal or conservative internal body models. Interindividual differences are a well-known aspect of RHI, with 66-80% of subjects experiencing the illusion (Durgin, Evans, Dunphy, Klostermann, & Simmons, 2007; Capelari, Uribe, & Brasil-Neto, 2009;

note that in the original work by Botvinick and Cohen, 1998, prevalence was reported to be as low as 42% and, therefore, is very likely to rely on the quality of the stimulation delivered) and mean ownership ratings spanning below maximal ratings (e.g. Siedlecka, Klimza, Łukowska, & Wierzchoń, 2014, Capelari, Uribe, & Brasil-Neto, 2009; however, to the best of the author's knowledge, a comprehensive study dedicated to ownership ratings has not yet been carried out). This is foreseeable from the perspective of multisensory integration theory: because of the existing spatial discrepancy between visual and tactile signals, incomplete fusion should take place, with stronger illusions occurring for prior distributions with better-defined peaks and weaker or non-existing illusions for wide, flat prior distributions. Individual prior distributions may differ for various reasons: I propose individual temporal binding windows and spatial tactile acuity as potential factors underlying interindividual differences in RHI; however, this list is certainly not complete.

A temporal binding window is the maximal tolerable asynchrony between signals for a cognitive system to judge them as occurring simultaneously. Synchronous and asynchronous stimulation in RHI can be redefined as occurring, respectively, inside and outside individual temporal binding windows, which have been shown to vary among people (Costantini et al., 2016). Interestingly, as the delay between visual and tactile signals increases, the subjective strength of the illusion tends to diminish but the variability of reported illusion strengths increases (Shimada, Fukuda, and Hiraki, 2009), which suggests that even for large delays between visual and tactile signals, they may fall within a liberal temporal binding windows (Costantini et al., 2016). Asynchronous stroking is well-known to entail some diminished form of the illusion (e.g. Guterstam, Petkova, & Ehrsson, 2011). Slight temporal discrepancies during RHI elicitation are also expected, particularly in manual stroking procedures; however, whether automated procedures yield stronger illusions remains unclear, with various results being reported (e.g. Rohde, di Luca, & Ernst, 2011; Rohde, Wold, Karnath, & Ernst, 2013). Individual temporal binding windows may also be crucial for illusion strength indices based on differences between synchronous and asynchronous conditions (e.g. Tsakiris & Haggard, 2005; Tsakiris, Prabhu, & Haggard, 2006).

Speculatively, other interindividual differences may come from differences in PPS size or in individualized patterns of perceptual processing of various kinds of sensory information, resulting in distinct weight ascription patterns. Spatial tactile acuity, defined as the ability to discriminate the spatial structure of surfaces (e.g., orientation of embossments) coming in contact with one's skin (Peters, Hackeman, & Goldreich, 2009; van Boven & Johnson, 1994), may be of particular importance here. It is very likely to be related to sensitivity to discrepancies between stimulation orientations, which have been shown to play an important role in RHI (Costantini & Haggard, 2007). Spatial curvatures of stimulation patterns on both hands may not overlap exactly, particularly in manual stroking procedures (due to the inexact placement of both brushes, slight discrepancies in stimulation orientations, and morphological differences between hands and dummies) – and such mismatches may be detected or "ignored", depending on the participant's tactile acuity. Tentatively, the increased weighting of tactile signals should also be observed in people with high tactile discrimination skills, resulting in diminished proneness to RHI. Large individual differences in this ability have been observed, both between same-aged subjects and between younger and older adults, as spatial tactile acuity tends to decrease with age (Vega-Bermudez & Johnson, 2004). This may also be related to morphological features, such as finger size (Peters, Hackeman, & Goldreich, 2009) or skin conformance (Vega-Bermudez & Johnson, 2004).

5.2. Multisensory integration hypothesis vs the Bayesian model developed by Samad et al. (2015)

Samad, Chung, and Shams (2015) were the first to propose a model in which self-recognition is driven by Bayesian sensory inference. This model shares crucial characteristics with the one presented above: an inference about the commonality of causal origin is based on the properties of sensory signals (location, time, and variance) and the prior probability of a common cause. As such, it addresses the problem of multisensory integration in a twofold way, pertaining both to the correspondence problem and the maximally efficient integration of sensory signals. The model provides an elegant mathematical description of the computational principles underlying RHI, reproduces phenomena described in the literature (e.g. the sudden onset of the illusion in PPS), and generates testable predictions.

However, important differences between the models may be indicated. The cognitive multisensory integration model – as outlined above – does not provide computational operationalization, but it does significantly widen the scope of factors taken into consideration. For example, Samad and colleagues (2015) fixed the prior probability value ($p = 0.5$), neglecting the role of Bayesian Coupling Priors. Since the prior value is set to 0.5, the commonness and separateness of causes are a priori equiprobable; therefore, in their model the illusion is actually bottom-up driven as it relies solely on the properties of sensory signals. In the multisensory integration account, prior probabilities vary depending on individual models encoding couplings between different sensory cues. These models are experience-informed and, therefore, idiosyncratic – the degree of relatedness may be interindividually variable. For example, people may differ in proneness to “large rubber hand illusion” (Pavani & Zampini, 2007) depending on the coupling strength between size (provided by visual cues, changed in comparison with one’s real hand) and weight (provided by proprioceptive cues, unchanged). Even more importantly, prior values should rely on individual parameters directly pertaining to the spatiotemporal characteristics of the stimulation, such as the scope of the temporal binding window (determining what actually is synchronous; Costantini et al., 2016) and, speculatively, other factors such as spatial tactile acuity (analogously, providing an idiosyncratic definition of what kind of stimulation is spatially congruent in the hand-centred reference frame) or PPS size (defining the boundaries of the interface of potential interactions with the world). Samad and colleagues (2015) themselves seem to acknowledge that prior probabilities should differ across people, as they write about an individual "tendency to integrate signals" (p. 19); however, what exactly hides behind this tendency remains unclear.

Moreover, the list of relevant sensory stimulation properties seems to be overly restrictive as well. In the Bayesian sensory inference model (Samad, Chung, & Shams, 2015), a cognitive system samples information only about location and timing, with spatial information being provided solely by visual and proprioceptive cues, and temporal information by visual and tactile cues. This seems to be an oversimplification: location is understood as necessarily being computed in the process of spatial remapping to external coordinates. In other words, the emergence of RHI depends on the degree of discrepancy between locations of sensory signals *in external space*, but the degree of discrepancy *on the body* is deemed irrelevant (or rather, assumed to be equal to 0). Recently, the term "skin space" ("S-space") has been coined (Haggard, Cheng, Beck, & Fardo, 2017; Cheng & Haggard, 2018; Fardo, Beck, Cheng, & Haggard, 2018) to describe a spatial representation allowing tactile localization on the surface of the skin. S-space may be understood as a tactile analogue of a visual field: it allows computations of spatial relations between various points on the body on the basis of topological information stemming from neighboring relations between receptive fields. Cheng and Haggard (2018) suggest that such a space may be sufficient for body spatiality to arise.

What are the implications of the concept of a skin space for RHI? S-space allows the smooth tracking of a tactile stimulus moving across the body part (Haggard, Cheng, Beck, & Fardo, 2017). I suggest that, in the process of multisensory integration, the visually tracked movement of a brush on a dummy is compared to a tactile path felt on a real hand. This may actually be much more relevant spatial information for embodiment than location in external space and it is entirely touch-driven. In the Bayesian bottom-up model (Samad, Chung, & Shams, 2015), touch does not provide spatial information; therefore, "illusion" and "no illusion" conditions must be differentiated on the basis of varying degrees of visuoproprioceptive (in)coherence (given that temporal information is constant). In the proposed multisensory integration account, tactile modality is crucial for both temporal and spatial information; we can even talk about "tactile takeover", because the degree of match between visual and tactile 3D spatial curvatures of stimulation in the hand-centred reference frame may be much more important than online proprioceptive information. It is also worth noting that tactile information significantly modulates proprioceptive assessments (Kuling, Brenner, & Smeets, 2016; Rincon-Gonzalez, Buneo, & Tillery, 2011). For a detailed discussion of the role of proprioception in RHI, see chapter 6.1.

To sum up, the computational rigor presented by Samad and colleagues (2015) is the right path to follow, but the multisensory integration mechanism underlying RHI is much more complex. Most importantly, more factors should be included in future models, nuancing both prior probability values and intersensory interplay of bottom-up flowing cues. The differences between internal body model hypothesis, bottom-up Bayesian model and multisensory integration model proposed in the paper are summarized in Table 1.

THEORY	TOP-DOWN INFLUENCES	SPATIAL INFORMATION	TEMPORAL INFORMATION	INDIVIDUAL DIFFERENCES	ROLE OF PROPRIOCEPTION
Internal body model hypotheses (Tsakiris 2010; 2017; Apps & Tsakiris, 2014)	Stem from the knowledge of one's own body and context, operationalized as Bayesian prior beliefs	Provided both by tactile (hand-centered reference frame) and proprioceptive modality (hand's location in external space)	Reduced to information about synchronicity/ asynchronicity	Stem from idiosyncratic (liberal/ conservative) and generative body models of the world and one's body	Unclear; illusion arises as a result of integration visual, tactile and proprioceptive information; proprioceptive prediction errors crucial for active inference
Bottom-up Bayesian model (Samad Chung & Shams, 2015)	Absent	Provided by proprioceptive modality	Reduced to information about synchronicity/ asynchronicity	Stem from individual tendency to integrate signals	Sole provider of relevant spatial information (about hand's position in space)
Probabilistic multisensory integration theory as presented in the paper	Stem from the knowledge of associations between intra- and intersensory cues; operationalized as Bayesian Coupling Priors	Provided both by tactile (skin space) and proprioceptive modality; visuo-tactile spatial congruency seems to be of a greater importance	Information about discrepancy between visual and tactile signals in reference to individual temporal binding windows; information about correlation of temporal structures	Stem from individualized patterns of sensory processing e.g. scope of temporal binding window, spatial tactile acuity, PPS size	Constraints the area of potential embodiment; influence of online proprioceptive signals is limited; information about hand's orientation potentially relevant

Tab. 1. Comparison of internal body model hypothesis, bottom-up Bayesian model and probabilistic multisensory integration model as presented in the paper

5.3. Rubber Hand Illusion, Maximum Likelihood Integration and probabilistic multisensory integration

The current models of appearance-based self-recognition acknowledge the importance of multisensory integration as well. For example, Apps and Tsakiris (2014, p. 95) write that "recognising one's self is a process of associating the unimodal properties of the body (i.e., the visual properties of one's hand), with other information about the body from any sensory system". However, they stress the body-relatedness of multisensory information which is deemed unimportant in the presented account. In particular, body-related visual information is replaced by a visuotactile congruence and knowledge of the structural properties or anatomical plausibility is reconceived of as visuoproprioceptive congruence. Coupling priors pertain to the properties of stimulation (which sensory signals tend to go together and what is the strength of their relationship) and are agnostic about the nature of an object. Nonetheless, the internal body model hypothesis predicts a large set of fundamental morphological constraints – including the material presence, human-like appearance and shape of the hand, presence of fingers, coherent laterality or gender, and possibility of embodying only one arm at a time – all of which have been shown to be irrelevant for embodiment. When top-down morphological constraints stemming from the putative knowledge of the body are removed, the curious plasticity of human self-recognition system may be explained with sole reference to multisensory integration rules.

“Visual drift” and “additional limb” phenomena may be used to show how multisensory integration theory may account for phenomena inexplicable from an internal body model hypothesis perspective. According to Tsakiris (2010), as a result of sustained congruent stimulation, visual capture of tactile signals takes place: somatosensory coordinates are shifted into a visual reference frame. This may be conceived of as a “winner-takes-all” mechanism where visual signals simply dominate tactile signals. This view is thought to be justified by the presence of a reproducible “proprioceptive drift” effect (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). After RHI elicitation, estimations of the actual position of one’s hand are skewed towards the rubber hand. However, proprioceptive drift is only partial as the real hand is localized in-between two hands rather than in the location of a rubber hand; as such, it is believed to be a causally unrelated correlate of the illusion (Abdulkarim & Ehrsson, 2016). The “winner-takes-all” view may also be challenged with the reference to recent reports showing that visual representation of a rubber hand is shifted towards the real hand's position as well (Erro, Marotta, Tinazzi, Frera, & Fiorio, 2018; Fuchs, Riemer, Diers, Flor, & Trojan, 2016). When asked to localize the position of a *rubber* hand (either with the use of a verbal report or the movement of a contralateral arm), participants tend to slightly mislocalize it in the direction of the real hand. This is consistent with the Maximum Likelihood Estimation rule: in the process of multisensory integration, a weighted estimate, resulting in a unified percept, is obtained, with combined spatial representation being localized closer to the rubber hand because of higher weights ascribed to visual signals. Note, however, that the spatial representations of the two hands converge towards each other but do not completely overlap. This may be caused by the fact that, due to the spatial discrepancies between visual and tactile signals, the fusion is incomplete and the cognitive system retains access to unimodal estimates (and uses this information while performing the task; van Dam, Parise, & Ernst, 2014). Erro and colleagues (2018) speculate that incomplete convergence may come from a cognitive bias: top-down knowledge of the placement of both hands prior to experimental manipulation.

The probabilistic multisensory integration framework may also be used to model the "supernumerary limb" phenomenon. Employing a double paintbrush setup, Ehrsson (2009) has shown that tactile sensations may bifurcate: when two visible right rubber arms were stimulated in synchrony with an occluded real hand, participants reported two distinct yet simultaneous feelings of being touched on both hands. Guterstam, Petkova, & Ehrsson (2011) replicated this finding in a slightly modified experimental setup: they placed an additional limb directly beside the visible real hand and confirmed the additional limb phenomenon with the use of self-report measurements as well as physiological recordings. Importantly, the duplication of touch referral results in attenuation of the sense of ownership spread over particular hands, as if the total amount of sense of ownership was divided rather than doubled. This may be explained by a bimodal distribution of location estimate – in the face of ambiguous sensory evidence, signals are equally likely to emerge from two spatial locations, which results in the sense of ownership being split into both hands (Ehrsson, 2009; Guterstam, Petkova, & Ehrsson, 2011). This is why both fake hands have to be at the same distance from one's real hand (or both rubber and real arms should be placed at the same distance from one's shoulder) for the "additional limb illusion" to occur (Folegatti, Farnè, Saleme, & de Vignemont, 2012).

6. Future Challenges and Empirical Validation

Two major challenges for the multisensory integration theory may be indicated. The first one pertains to the exact role of proprioceptive signals in RHI, which remains unclear. The second one concerns the distinction between action and passive perception in the context of embodiment.

6.1. The role of proprioception

Proprioception is frequently assumed to be a constraint of RHI. The illusion occurs only if the distance separating the hands is shorter than 30cm (Lloyd, 2007) and the rubber hand must be placed within peripersonal space for the illusion to arise (Blanke, Slater, & Serino, 2015). However, the extent to which online proprioceptive signals contribute to the illusion may be smaller than previously thought. Certain visuoproprioceptive coherence is necessary (since anatomically implausible rubber hand positions and large hand orientation mismatches eliminate the illusion; Ehrsson, 2012). On the other hand, Abdulkarim and Ehrsson (2016) have shown that mechanical displacement of the participant's hand during illusion elicitation (either towards or contrariwise to the rubber hand) does not influence the strength of the illusion. In their interpretation, the causal role of proprioception is limited, since the illusion is not dependent on shifting proprioceptive representations. Moreover, the onset of the illusion in PPS is abrupt and the strength of the illusion is not related to the distance separating the hands as long as they are both placed within PPS.

In our lab (Motyka & Litwin, in preparation)[3], we observed that RHI strength did not differ for small (8 cm) and large (24 cm) discrepancies between locations of the hands. More importantly, proprioceptive accuracy – operationalized as a mean absolute difference between initial and reproduced positions in a task requiring repeated active reproduction of one's arm position (Lubiatowski et al., 2013) – was not a significant predictor of illusion strength, both in "close" and "far" conditions. Bayesian Factor analyses confirmed that our results reflected genuine null effects rather than experimental insensitivity. Taken together, it seems that weighting of proprioceptive signals (which should be higher for participants with high proprioceptive accuracy) does not influence the illusion strength and, therefore, the relevance of proprioception in multisensory integration processes underlying RHI onset is minimal. These observations are in stark contrast with predictions generated by the model proposed by Samad and colleagues (2015, p. 19). In particular "[the] model predicts that the illusion is stronger the nearer the fake and real hand are to each other [and] the noisier the proprioception modality is."

This is yet another point of disagreement between the multisensory integration account and the Bayesian sensory inference model (Samad, Chung, & Shams, 2015): the latter puts a strong emphasis on the role of proprioception. This is a natural consequence of the fact that tactile modality does not provide spatial information – in the absence of temporal information (the "no stroking" condition), the occurrence of the illusion should rely solely on integration of

[3] The code used for data analysis is available on GitHub at https://github.com/Pawel-Motyka/RHI_proprioception

visuo-proprioceptive spatial estimates. Given the relatively large variance (low precision) of proprioceptive signals, RHI should arise when the "distance between the real hand and rubber hand is not very large (…), at least for those individuals who do not have very precise proprioceptive representations" (Samad, Chung, & Shams, 2015, p. 7). This prediction has been confirmed, as 73-88% of the participants experience the illusion without tactile stimulation (Samad, Chung, & Shams, 2015). How may these findings be reconciled with reports showing a very limited influence of online proprioceptive signals on RHI (Abdulkarim & Ehrsson, 2016; Motyka & Litwin, in preparation)? Perhaps the relevance of online proprioception is restricted to a particular kind of proprioceptive information (e.g., pertaining to hand orientation) or surfaces only in the absence of tactile information – e.g., the cognitive system switches to proprioception when it lacks information pertaining directly to where body boundaries are. An even more radical idea is that proprioception is not even a substitutionary modality, but merely a supplementary modality – visuoproprioceptive coherence strengthens the illusion (Costantini & Haggard, 2007) just like audio-tactile (Radziun & Ehrsson, 2018a) or visuo-interoceptive (Suzuki, Garfinkel, Critchley, & Seth, 2013; Aspell et al., 2013) coherence, boosting the degree of intersensory congruence in general. This remains a subject for future investigation.

6.2. Active vs. passive condition

The multisensory integration model, as outlined above, pertains to the passively induced sense of ownership (like in the classic RHI setup). Active conditions further diminish the importance of appearance,[4] since the sense of ownership results from sensory feedback matching the predicted input rather than spatiotemporal coherence of stimulation. Therefore, constraints on passive induction methods (e.g., hand shape) are irrelevant in active conditions for which factors such as coherence of spatiotemporal properties of movement or coherency of tactile input resulting from contact with another object seem to play the major role. As a result, the sense of ownership may be spread over objects strikingly different than one's own body part (Ma & Hommel, 2015a; b) – the embodiment of a 2D rectangle would be very unlikely to arise from mere visuotactile stimulation.

However, this does not necessarily mean that the multisensory integration model – as outlined above – posits two different underlying mechanisms for embodiment driven by passive stimulation and active exploration. The multidimensional intersensory contingencies revealed in the latter are simply very challenging for modeling. As opposed to passive elicitation, visuomotor paradigms vary considerably, with idiosyncratic environments and objects being used. More importantly, additional sources of information (e.g., efference copies and other efferent signals) should be included in the model. It needs to be stressed that the multisensory integration account is largely agnostic as to whether active induction of the sense of ownership relies on a different mechanism. It is actually unlikely to do so: embodiment has been shown to result from the integration of different combinations of multimodal signals, e.g. tactile-proprioceptive (the somatic rubber hand illusion; Ehrsson, Holmes, & Passingham, 2005; Radziun & Ehrsson, 2018b) or visuo-proprioceptive (Walsh, Moseley, Taylor, & Gandevia, 2011; Samad, Chung, & Shams, 2015). Visuomotor elicitation may be one of various possibilities – based on the integration of different kinds of information and is computationally more complex, but 'qualitatively' similar.

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[4] See Ratcliffe & Newport (2017) for a report of attenuated illusion for distorted hand-like objects in mediated-related conditions. However, in this study, the virtual environment was not explored (as opposed to e.g. Ma &

The curious relation between action and body perception has recently been explored by Aymerich-Franch and Ganesh (2016) who propose that internal body models refer to functional structural properties of the body. According to their Gibson-inspired functional body model hypothesis, external objects may be embodied if their physical properties are sufficient to afford actions that the brain ascribes to the bodily counterpart of a to-be-embodied-object. Interestingly, it is sufficiency rather than correspondence that matters: objects that allow new actions can be embodied. Therefore, people may embody larger hands but tend to reject the smaller ones (Pavani & Zampini, 2007); smaller hands significantly constrain action possibilities, whereas larger hands do not (see also experiments on robotic arms performed by the researchers, e.g. Aymerich-Franch, Petit, Ganesh, & Kheddar, 2017a). This view corresponds with the classic accounts of body schema extension (Merleau-Ponty, 1962), e.g., the embodiment of navigation-affording rods by blind people. Note, however, that some of the reports may be problematic to explain from this perspective (e.g. 2D rectangles or balloons significantly constrain action possibilities and do not allow new ones; Ma & Hommel, 2015a). Reconciliation of the functional body hypothesis with multisensory integration theory – so they could collectively, comprehensively account for the experimental results obtained both in active and passive paradigms – remains an interesting future challenge.

6.3. Experimental predictions

While contemporary approaches underline the importance of the appearance of a to-be-embodied-object (Tsakiris, 2010; Apps & Tsakiris, 2014; Azañón et al., 2016; Ratcliffe & Newport, 2017; Blanke, Slater, & Serino, 2015), in the proposed model this is considered to be

Hommel, 2015a) as participants' activity was restricted to tapping with an index finger.

irrelevant. Past experiments on the effect of appearance failed in preventing concurrent reduction of the degree of intersensory matching (Ma & Hommel, 2015a). As such, they cannot be interpreted as providing support for the internal body model hypothesis. In this section, I would like to pre-register an experiment allowing disambiguation between competing theories through the manipulation of an object's appearance without a simultaneous influence on any of its stimulation-related properties.

The experiment would employ the gradual likening paradigm used by Tsakiris, Carpenter, James, and Fotopoulou (2009). However, unlike in their study, the participant's hand and all of the objects would be matched in terms of weight, volume, underlying surface area, layer ("skin") conformity, orientation, and shape to allow the trajectory of brushstrokes be parallel. Note that such an experimental paradigm would require the separate preparation of a set of objects for each individual participant. Objects would be gradually likened via the progressive addition of hand-like features in the finger area – for example, a fingerless hand-shaped mass (object 1), would be likened to a hand through the chiseling of channels imitating fingers closed together (object 2) and addition of other finger features (e.g., fingernails, joints dividing fingers into distal, middle, and proximal phalanxes; object 3). Importantly, subjects would be asked to keep their fingers together. Then, a spatiotemporally congruent stimulation would be delivered to the area over the knuckles and the corresponding area on the objects. In this setup, intersensory matching does not decrease in the process of likening as all of the objects are designed to "feel like one's own hand". For all objects, spatiotemporal stimulation patterns would be kept unchanged and any tactile and proprioceptive signals expected would be coherent with actual signals from the hand. As such, the distribution of the coupling prior should not change in the process of likening. Such an experimental paradigm would let us adjudicate between competing models, as any differences in the sense of ownership between conditions would count against the multisensory integration model as outlined above. However, the lack of significant differences would count against internal body model hypothesis (Tsakiris, 2010, 2017; Apps & Tsakiris, 2014). Optimally, the experiment should be carried out in between-subject design to prevent any carry-over effects or response bias (since participants would be very likely to feel obliged to report that the sense of ownership is stronger in the case of the more hand-like object).

7. Concluding Remarks

In this paper, I have proposed a novel multisensory integration account of how the sense of ownership arises based on the passive elicitation paradigm of RHI. This model is the first to provide a thorough description of RHI in terms of multisensory integration laws and rules, such as Maximum Likelihood Estimation, Bayesian Coupling Priors, and correlation of temporal structures. Some important differences between the proposed account and the currently dominant theories of RHI may be indicated. As opposed to the internal body model theory (Tsakiris, 2010; 2017; Apps & Tsakiris, 2014), it disposes of the need for any top-down modulations carrying information that do not directly pertain to properties of stimulation or relations between sensory cues (e.g., knowledge about the appearance of one's body part or anatomy). In the presented view, multisensory integration processes are not only necessary, but also sufficient for RHI to occur. Moreover, as compared to the Bayesian Sensory Inference model (Samad, Chung, & Shams, 2015) and other multisensory integration accounts (e.g. Ehrsson, 2012), it significantly broadens the scope of relevant factors and grants even more significance to tactile modality; it is reconceived of as a provider of the skin-based spatial information that is most relevant for embodiment. The model accounts for a wide range of phenomena described in the literature (in particular, for the enormous plasticity of human body image) and generates testable predictions.

These predictions may be directly tested using experimental paradigms which actually discriminate between competing theories.

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Graphical abstract