Body-ownership and the experimental psychology of the self

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Abstract

Human experimental psychology seems inextricably bound up with a notion of self, or individual mental life. The link between self and body has always been acknowledged, but psychologists had few ways to investigate, analyse or understand this link. As 2025 marks the 50th birthday of *JEP:HPP* and twenty years since the publication of our "Re-visiting the rubber hand illusion" paper in the journal, we take this opportunity to reflect on the impact, reach, and major developments that followed its publication. In particular, we focus on how the methods and theoretical constructs from our paper have extended the concepts of bodily self-awareness towards other fields beyond experimental psychology. Our paper helped to develop experimental approaches to understanding the role of the body in self-awareness, and mental life more generally. The combination of rigorous experimental methods and a clear theoretical model has allowed psychologists to have a clearer view of the relation between body and self.

Public Significance Statement

The link between self and body has always been acknowledged in the history of ideas, but psychologists had few ways to investigate, analyse or understand this link. The Rubber Hand Illusion has allowed psychologists to study this link scientifically. We review methodological and conceptual investigations that have advanced our understanding of the mechanisms, processes and consequences that link the sense of self to the body. The findings have allowed us to understand the ontogenetic development of body-awareness, some of the causes and effects of altered states of body-awareness, and the importance of the representation of one's body for social cognition.

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1. Introduction

In 1998, Mathew Botvinick and Jonathan Cohen (Botvinick & Cohen, 1998) published a 1-page article in *Nature* describing an illusion in which tactile sensations are referred to a rubber hand. They suggested that a three-way interaction between vision, touch and proprioception can form the basis of bodily self-identification and bodily awareness, or, as it came to be known, the sense of body-ownership. A number of studies reprised and extended the basic effect reported by Botvinick and Cohen, but it was only in 2004-5 that the rubber hand illusion emerged as a key paradigm for studying the relation between body and self. This was in large part due to two papers published within a half a year of each other, in which experimental psychology and cognitive neuroscience realized the full potential of this illusion to serve as an empirical model of bodily self-awareness. Our paper published in the *Journal of Experimental Psychology : Human Perception and Performance* (Tsakiris & Haggard, 2005) and the paper by Ehrsson, Spence and Passingham (Ehrsson et al., 2004) published in *Science* catalysed a particular fruitful research programme on understanding the mechanisms, processes and consequences that underpin the fundamental identification of one's self with one's body.

As 2025 marks the 50th birthday of *JEP:HPP* and twenty years since the publication of our paper in the journal, we take this opportunity to reflect on the impact, reach, and major developments that followed its publication. Re-reading our paper some 20 years after the experiments were done prompts a longer and broader view than is normal. Our paper may have been useful in developing an experimental approach to how the body figures in mental life, so we will begin with a theoretical overview of this question. Then, after briefly reviewing the original study, we use its findings as a springboard to discuss its impact and reach in relation to current psychological research on body representation and bodily self-awareness.

2.Psychology as the study of the bodily self

Psychology is traditionally described as the study of the mind. This definition already puts the discipline in an uncertain place with respect to the body. Deeply-embedded dualistic notions have made mind and body seem distinct, although even René Descartes clearly recognised that there must be a distinctive relation between them. Psychology's paradigmatic comment on the body is James' description of the "feeling of the same old body always there" (James, 1893). By this, James meant that one's body is a constant background to all one's mental life. The body is perhaps the dominant component of the "free water of consciousness that psychologists resolutely overlook". Thus, having a body is an enabling condition for having mental states – brains in vats are thought-experiments, not actual experiments.

The history of psychology shows surprisingly few attempts to investigate directly how the body contributes to the mind. Several traditions of somatosensory physiology and psychophysics, focussed on the peripheral origin and central processing of specific bodily sensations – yet this work studied the encoding of external *stimuli* impinging on the body's sensory receptors. The body itself became, again, part of James' puzzling background to mental life. While the body is the *locus* of experience in studies of touch, temperature etc., the *content* of experience is typically externally attributed. Tactile experience is an experience *of* some external object that the body touches, rather than an experience *of* one's body. One exception may be Katz's (Katz & Krueger, 2016) work on the duality of touch.

In contrast, the muscular sensations that signal the relative spatial positions of body parts are clearly proprioceptive rather than exteroceptive. However, early work on muscle spindles focussed on their role in reflex coordination of posture movement, and largely ignored conscious states. The psychological significance of proprioception remained unrecognised until Lackner's seminal studies used tendon vibration to show that experimentally-induced conflicts between muscular

proprioceptive sensation and other inputs produced compelling distortions in the sense of one's own body (Goodwin et al., 1972; Lackner, 1988).

A second tradition concerns the study of the autonomic nervous system, and the regulation of the internal milieu. Again, William James played a key role, noting that cardiac and visceral receptors produce distinctive bodily sensations, as well as providing the afferent information to the circuits that make up the autonomic nervous system. Somatic sensations continue to play a critical role in the psychology of emotion.

A third tradition, which perhaps lies closest to our experimental work in 2004, comes from comparative cognition, specifically primatology. It focusses on the representation and awareness of one's own body as a specific and unique physical object. Humans and other animals' responses to seeing themselves in a mirror have been noted since classical times. However, Gallup appears to have been the first to apply a clear experimental protocol, based on applying a visible mark to the face of anaesthetized chimpanzees (Gallup, 1970). If the animal subsequently attempted to remove the mark upon viewing itself in a mirror, Gallup reasoned that the animal must have a form of self-awareness. It must recognize that what it sees in the mirror is its own body, its own face, and therefore a mark on it*self*. Current scientific consensus suggests that such mirror self-recognition can only be one component of self-awareness, rather than a defining or necessary condition. However, Gallup's approach clearly suggests a strong relation between self-awareness and *visual* recognition of one's own body. To pass the test, an animal must identify that its experiences, its *self*, are linked to a physical body that can be visually discriminated from other objects. Although not a formal requirement of the rouge test, it seems clear that mirror self-recognition must involve matching between what is seen in the mirror, and what is known from somatic information. In particular, animals and other humans seem to use the synchrony between movements they make, and the movements they see in the mirror, to deduce that they are seeing the same body that they feel they are moving.

Self-awareness is then the recognition that one's self and one's experiences are tied to one particular physical object, namely one's own body, rather than other bodies, and not just because of visual recognition. Further, this object is characterised by a special kind of multisensory convergence, in which visual and somatic information are coherent. Gallup's work suggested that visual-somatic correspondence may be necessary condition for self-awareness. More generally, mirror self-recognition suggests the importance of body and bodily sensation for the sense of self. This contrasts with other psychological traditions that emphasise rather higher-level cognitive functions such as autobiographical memories and narratives, or social relations, as the basis of self (for a review see Gillihan & Farah, 2005). As we will explain below, studies of such bodily illusions have allowed researchers to progress beyond a purely visual concept of self- or body-recognition towards a more multisensorial understanding of body-ownership.

3.The rubber hand illusion as an experimental manipulation of self-awareness

The rubber hand illusion (RHI), in contrast, appeared to suggest that visual-somatic correspondence is *sufficient* for self-recognition. The core of the RHI involves the participant observing a rubber hand on a table in front of them being stroked by a brush, while their own hand – which is hidden from view – is being stroked by a second brush in the same way, and at the same time as the rubber hand. Because the participant sees a hand being stroked, and feels their own hand being stroked in the same way, the brain – it is argued – infers that the hand being viewed is the participant's own hand. This finding has profound implications for the psychological concept of self, as Botvinick and Cohen noticed in their original paper (Botvinick & Cohen, 1998). In particular, it suggests that a sense self can be established "bottom-up", simply through repeated experience of correlated events across different modalities. Interestingly, visual object recognition (or, strictly, misrecognition, since the rubber hand is incorrectly taken for the participant's own) therefore lies at the heart of the concept of sense of self emerging from RHI, just as in earlier work on mirror self-recognition.

Botvinick and Cohen had designed a simple questionnaire designed to capture the highly unusual experience that seems to occur in the RHI. They had also shown that the perceived position of the participant's hand is displaced towards the rubber hand. This displacement can be understood in terms of the different signals that the brain receives during the RHI event. Synchrony between visual and tactile input leads the brain to attribute visual and tactile events to a single common source – a process known in computational theories as 'causal inference'. Common source attribution implies that visual and tactile input must arise from a single location in space, namely the location of one's hand. However, the information about current hand position provided by proprioceptive position sense conflicts with visual information about the location of the rubber hand. In resolving this conflict, the brain relies on visual information, and adapts proprioceptive position sense, so that the participant's hand feels closer to the rubber hand than it really is. This account links the RHI to other examples of intersensory learning, such as prism adaptation (Redding et al., 2005). The relation between proprioceptive drift and explicit judgements about sense of body ownership (for example, through questionnaires) remains controversial. Changes in proprioception sensation can occur without changes in body-ownership, for example during normal voluntary movement. However, in the context of the RHI, altered experiences of body-ownership are often accompanied by changes in proprioception (Aimola Davies et al., 2013; Farmer et al., 2012; Riemer et al., 2015, 2019; Rohde et al., 2011; Tsakiris, Carpenter, et al., 2010). The only meta-analysis to date suggests that the available evidence strongly favours the presence of a correlation between subjective embodiment and proprioceptive drift (Tosi et al., 2023)."

Key computational theories (Ernst & Banks, 2002) model proprioceptive adaptation as a multisensory cue-combination problem, in which visual and proprioceptive information about hand position are combined to provide a single estimate, by weighting each source according to its reliability. The shift in proprioceptively-perceived position towards the rubber hand reflects the higher precision of visual information compared to proprioceptive information. Put another way, vision dominates the cue combination process. This logic works on the assumption that causal

inference precedes cue combination. That is, the brain must first link the visual input and tactile stroking to a single common source event. The involvement of touch sensation further implies that this source event involves one's own hand. Interestingly, the sense of touch therefore seems to dominate the causal inference part of the process, even though vision dominates the cue combination process. Only once a common cause is established does the viewed location of the rubber hand become relevant to deciding where one's own hand is located. That is, common cause inference is a necessary condition of cue combination. Thus, if the perceived position of the hand changes from before to after stimulation, the extent of this change can be taken as a quantitative, implicit marker of the causal inference assumption that attributes visual and tactile stroking inputs to a common source, i.e., the rubber hand is part of oneself.

The RHI has since become a central method for experimental investigation of bodily self-awareness. Our research (Tsakiris & Haggard, 2005) perhaps contributed to this development in a number of ways. These included a specific theory of measurement, and a focus on the necessary and sufficient conditions of the experience of body-ownership.

4. Methodological advances in the study of body-ownership

It is a commonplace of psychology that mental states are difficult to measure. Moreover, as James noted, the familiarity and background-ness of one's own body may make the relation between body and self particularly difficult to measure. In our 2005 paper, we developed the use of proprioceptive position sense as a valuable measure of the RHI. Botvinick and Cohen had already reported that inter-manual reaching was altered by the illusion. However, our paper appears to have been the first to systematize judgements of hand position as a direct measure of the change in bodily self-awareness. Briefly, the shift in perceived hand position towards where the rubber hand was seen gave a quantitative yet implicit measure of the key psychological construct underlying the illusion, namely the representation of one's own body as a physical object. The first important innovation was the presentation of a ruler with variable offset on a blank visual background, for participants to

indicate the perceived position of their hand. This helped to reduce perseveration in measures of proprioceptive position taken before and after visuo-tactile stimulation. Second, as in Botvinick and Cohen (1998) we also obtained and compared measures of proprioception taken before and after visuo-tactile stimulation but did so in a way that asked for purely perceptual, rather than motor, judgments. This allowed us to control for any general biases in proprioception and quantify the *change* in perceived hand position caused by multisensory stimulation.

A third innovation was the use, in some experiments, of coupled computer-controlled motors to precisely control visual and tactile stroking. This allowed us to have a physically-balanced control condition. By aligning the brushes on the two motors, or by misaligning one brush set by 180 degrees, we could deliver identical multisensory stimuli either synchronously or asynchronously. Synchronous stimulation provided evidence supporting causal inference, while asynchronous stimulation provided evidence against it. Crucially, contrasting synchronous and asynchronous condition could control for the mere effects of visual and tactile input. The difference between the proprioceptive drifts measured in synchronous vs. asynchronous conditions was used as a measure of the strength of the illusion, which we termed the *RHI effect*. Standardizing these procedures further allowed us to measure the RHI at regular time intervals as the RHI built up, describing for the first time the rate at which evidence of multisensory matching could accumulate towards a mental representation of self. The results pointed to a high degree of plasticity, with most of the proprioceptive adaptation occurring within two minutes of stimulation.

Over the years, additional psychophysical approaches advanced the field. For example, Costantini and colleagues (Costantini et al., 2016) demonstrated a clear relationship between individuals' temporal resolution and the time window within which the rubber hand illusion is experienced. More recently, Chancel et al.(Chancel, Ehrsson, et al., 2022) showed that sensory uncertainty contributes to the rubber hand illusion and that body ownership reports in psychophysics tasks fit a Bayesian causal inference model of multisensory combination (versus segregation). As we discuss in

later sections, early development of well-controlled experimental designs and careful measurement was adopted and enhanced by researchers in experimental psychology and other fields. These advances contributed to a wider and more grounded measurement model that could fully characterize the rich but elusive experience of one's own body, complemented by qualitative (Longo et al., 2008), physiological (Crucianelli & Ehrsson, 2022; Ehrsson, 2007; Slater et al., 2008) and neural (Ehrsson et al., 2004; Graziano et al., 2000; Tsakiris et al., 2007, 2008) data.

5. Theoretical advances in the psychology of body-ownership

Adopting a more robust methodological approach also enabled us to further investigate the necessary and sufficient conditions for the induction of the RHI and led us to conceptualize the rubber hand illusion as a *model instance* of the sense of body-ownership.

5.1. The top-down body

Botvinick and Cohen claimed that intermodal matching was sufficient for self-awareness. We made two important experimental observations that challenged this claim, and suggested that some other "top-down" factors were also necessary. We found that turning the rubber hand through 90 degrees, so that its posture was incongruent with the posture of the participant's hand, abolished and in fact reversed the RHI, as measured by the difference in proprioceptive drift between a synchronous and an asynchronous stroking condition. Viewing a *right* rubber hand being stroked while one's own unseen *left* hand was stroked had a similar effect, as did replacing the rubber hand with a block of wood. That is, when participants viewed the stroking being applied to an object that was not plausibly their hand, then synchronous visual-tactile stroking was insufficient to link the object to the self, and multisensory stimulation did not lead to any change in self-awareness. These results suggested that the brain maintains a clear prior model of what one's body is like. This prior is

presumably used at the causal inference stage to compute whether the visual stroking stimulation and the tactile stroking stimulation might reflect a single event, and thus whether the viewed object corresponds to one's own hand.

The internal model of the body contains at least a representation of possible postures, and a representation of visual appearance. This idea had been hypothesised before (Paillard, 1999), and indeed perhaps forms the basis for James "body always there". Our paper, however, showed a way that this internal stored model could be systematically investigated. These findings raise the interesting question of how the internal body model is assembled, over what timescale and from what signals. The "body prior" may simply reflect memory of previous intermodal correspondences. The body prior concept has some interest for various neurological psychiatric disorders that involve distortions of bodily self, including eating disorders (Eshkevari et al., 2012). Our study also suggested how targeted sensory experiences might be used to update an aberrant body prior.

5.2.Extension and spread

We have seen the importance of understanding that one's own body is a physical object. The self therefore has extension and occupies volume as other objects do. This raises the question of whether each part of the body is attributed separately to the self on the basis of its localised sensory inputs, or whether the attribution process is constrained to be spatially coherent. The parts of the body form a single continuous whole, and this continuity seems essential to the sense of self, as phantom limb phenomena show. We speculated that the mental representation of the body as a continuous object may be an important basic element of the coherence of the self generally. Few experimental studies, before or since, have dealt with the questions of local vs global aspects of bodily self-awareness.

We found that visual-tactile stimulation of the middle finger lead to a significant RHI effect when participants judged the position of the middle finger, but no such effect when participants judged the perceived position of the thumb. A further experiment found the same, purely local RHI effects

when stimulating either the finger or the thumb, and asking participants to judge the position of the index finger and the thumb. This pattern of results suggested a rather local process of assembling bodily self-awareness, with intermodal linkage supporting causal inference between individual sensory inputs. On this view, self-awareness should be a matter of a specific sensory experience located on a specific body part in focal attention. Other, unstimulated parts of the body do not seem to share the self-attribution of stimulated body parts. This localist view seems unable to capture the experience of a single, coherent and continuous self, and makes self-awareness heavily dependent on immediate stimulation. It therefore remains unclear how a coherent overall sense of self could emerge from merely local cross-modal correspondences.

In a separate experiment, we pursued this question further, by stimulating the index finger synchronously or asynchronously, while also stimulating the little finger synchronously or asynchronously. Participants judged the positions of the index, middle and little fingers in different blocks. Synchronous stroking of the index finger while the little finger was stroked asynchronously lead to an RHI effect, as measured by proprioceptive drift, for the index but not the little finger. This pattern of results was reversed when the little finger was stroked synchronously and the index finger asynchronously. This finding confirms that self-awareness from intermodal matching is indeed local rather than global. Interestingly, however, this experiment found a significant shift in the perceived position of the middle finger, which was never stimulated, when both index and little fingers were stroked synchronously, compared to when they were both stroked asynchronously. Thus, the local effects of intermodal matching on self-awareness had some degree of spread beyond the immediate stimulation site. The spread from one digit to its immediate neighbour might seem limited, and insufficient to explain the overall coherence of bodily self-awareness. However, outside the lab, multiple body parts constantly receive a diverse range of multisensory stimulation. Therefore, a mechanism of spread to nearest neighbours could be sufficient to produce and maintain a coherent representation of the body as a whole.

Starting from this original observation about the relatively fragmented body representation evoked by multisensory stimulation, we (Tsakiris et al., 2006; Tsakiris, Longo, et al., 2010) and others (Burin et al., 2017; Kalckert & Ehrsson, 2012, 2014a) contrasted the classical visuo-tactile RHI with an active agentic mode of inducing ownership over a rubber hand. We showed that localised proprioceptive drifts, specific to the stimulated finger, were found for tactile and passive stimulation. Conversely, during active movement of a single digit, the proprioceptive drifts were not localised to that digit, but were spread across the whole hand. Whereas a purely proprioceptive sense of body-ownership is local and fragmented, the motor sense of agency integrates multiple body parts into a coherent, unified awareness of the body. Importantly, as shown later, the sense of body ownership is equally strong across different combinations of sensory and motor cues. The combination of afferent and efferent signals that occurs in active movements resulted in the same illusion, namely that the viewed hand belonged to one's own body, as in purely passive visual-tactile stimulation (Kalckert & Ehrsson, 2014b). Other studies have also investigated the relation between experiences of body parts, vs. the body as a whole. A hierarchical probabilistic model was used to explain the part-whole relationship in multisensory body awareness (O'Kane et al., 2024).

Different combinations of sensory input can all lead to comparable phenomenological experiences of body-ownership. The links that emerged between the experimental research on the sense body-ownership with that on the sense of agency was also a catalyst for a more integrated perspective on embodiment: both experiences are important elements of self-awareness (Blanke & Metzinger, 2009; De Vignemont, 2011; Gallagher, 2000).

6. Impact beyond experimental psychology

The methods and theoretical constructs from our paper extended the concepts of bodily self-awareness in other fields beyond experimental psychology and enabled new lines of research aimed at refining the interactions between bottom-up and top-down factors. Below we outline some of these key advances brought about by the inspiring research of many colleagues across the world.

The first of these wider impacts has been in neurology (Fotopoulou et al., 2008; Garbarini et al., 2013) and neuropsychiatry (Eshkevari et al., 2012; Harduf et al., 2023). The RHI is now routinely used to research bodily self-awareness in different groups of patients. For example, clinicians studying body image disorders can now use well-controlled experimental approaches to understand how different sensory signals contribute to body image (Crucianelli et al., 2019; Eshkevari et al., 2012). Fotopoulou and colleagues were among the first to study body-awareness in patients with anosognosia (Fotopoulou et al., 2008) and somatoparaphrenia (Fotopoulou et al., 2011) using RHI. This approach brought experimental methods to bedside testing of cognitive neuropsychology. More recently, the same group investigated the relationship body ownership studied through the RHI and affective touch. They took a transdiagnostic approach including experimental, pharmacological, and neurostimulation studies in healthy individuals as well as behavioural and neuroimaging investigations in psychiatric and neurological populations. By systematically manipulating the velocity of tactile stimulation during the rubber hand illusion to increase the likelihood of activating the so-called C tactile system, they showed that affective touch led to greater perceived pleasantness and conscious feelings of ownership (Crucianelli et al., 2013, 2018). They further showed that these were effects of affectivity and certainty (not mere valence) of the congruency between seen and felt touch (Filippetti et al., 2019). They also extended these investigations to neurological populations (Jenkinson et al., 2013, 2020; Martinaud et al., 2017) to show that affective touch increases body ownership following right-hemisphere stroke, providing important neuroanatomical insights into the brain areas necessary for tactile affectivity and body ownership. Our findings had suggested that top-down prior body representations such as hand posture and left/right hand identity play a key role in the experience of body-ownership. Subsequent studies also showed that the rubber hand should be placed with the boundaries of visuo-tactile peripersonal space surrounding the hand (Lloyd, 2007). These concepts were also then used by researchers who focused on right-brain-damaged hemiplegic patients affected by an atypical form of hemisomatoagnosia. While not explicitly denying that their contralesional (left) limbs belonged to

themselves, these patients claimed that the examiner's left hand was their own whenever it was positioned on the table next to their real left hand (Garbarini et al., 2013). This arrangement recalls our finding that RHI effects tended to be stronger when the rubber hand complied with preexisting body representation constraints (Garbarini et al., 2014).

The second area of impact has been the extension from hands to other body parts, and indeed to the whole body. The first extension from body-parts to full bodies was enabled by research in Virtual Reality (VR) and the sense of presence. The research groups of Mel Slater (Maselli & Slater, 2013) , Henrik Ehrsson (Ehrsson, 2007; Petkova & Ehrsson, 2008) and Olaf Blanke (Lenggenhager et al., 2007) used the methods of the classic RHI to probe more global forms of body-ownership. Lenggenhager and colleagues extended the RHI to the full body. This involved modifying aspects of embodiment that were not altered in the RHI, such as the location of the self within navigational space. They used a similar experimental paradigm to ours, including comparable control conditions (i.e., a non-body object) and comparable behavioural measures (i.e., a perceived change in spatial position). The extension to full body illusions also enabled researchers to re-evaluate the concept of peripersonal space (PPS), that had until then been disconnected from the literature on body-ownership and bodily-self consciousness. The visuo-tactile stimulation used to trigger both the RHI and the full body illusion recalls the stimulation patterns that activate neurons encoding PPS (Brozzoli et al., 2012). This suggests that that the multisensory integration mechanism underlying bodily cues in PPS is also involved in bodily self-consciousness (Grivaz et al., 2017). The behavioral measures used in the full body illusion confirmed that peripersonal space is indeed the space of the self (Serino, 2019).

Around the same time, two new strands of research extended RHI research towards questions of identity and social cognition. With regards to personal identity, Tsakiris (Tsakiris, 2008) and Sforza and colleagues (Sforza et al., 2010) showed how inter-personal multisensory stimulation (IMS) that respects anatomical constraints and priors can lead to a change in the mental representation of

one's own face. In the Enfacement Illusion (Apps et al., 2015; Sforza et al., 2010; Tsakiris, 2008), watching another person's face being touched synchronously with one's own face lead to changes in self-face recognition. Specifically, the other person's face came to be perceived as more similar to one's own. The experimental design of these studies drew directly on our earlier RHI methods. Participants were stroked on their face while they were looking at the face of another unfamiliar individual being touched in synchrony or asynchrony. This procedure was termed Interpersonal Multisensory Stimulation (IMS). Before and after IMS participants performed a self-recognition task. The results showed that synchronized multisensory signals had a significant effect on self-face recognition: participants judged the other's face as physically more similar to their own after synchronous IMS (Sforza et al., 2010; Tajadura-Jiménez et al., 2012; Tsakiris, 2008). Participants also rated the other's face as more similar to their own following synchronous as opposed to asynchronous stimulation (Tajadura-Jiménez & Tsakiris, 2014; Tsakiris, 2008). Changes in the mental representation of one's own face as a result of the Enfacement Illusion are also accompanied by specific changes in underlying neural processing (Apps et al., 2015; Serino et al., 2015). The changes in judged similarity in the Enfacement Illusion suggested that participants' visual representations of their own and another's body had become partially overlapped, or shared. The synchronous IMS in enfacement elicits an overlap, or sharing, of body representations between self and other. This recalls the self-recognition task discussed in the introduction of the present paper.

With regards to social cognition and based on our original finding about the interaction between bottom-up and top-down effects on bodily self-awareness, a series of studies have investigated how multisensory integration could affect social cognition, in many cases building on the methods and results of our paper. As a first step, researchers looked at the relation between the RHI and body-image, defined here as the primarily conscious visual representation of the appearance of one's body. Longo and colleagues (Longo et al., 2009) showed that experiencing the RHI leads people to judge the rubber hand as more physically similar to their own hand. Importantly, apparent differences in the visual appearance between the participants' own hand and the rubber hand did

not influence the effect of the illusion. Next, Farmer and Tsakiris (Farmer et al., 2012) asked whether multisensory stimulation can lead participants to experience ownership over a hand having a different skin colour from their own. Results from two studies using introspective, behavioural and physiological methods showed that, following synchronous visuotactile stimulation, participants can experience body-ownership over hands that, on the basis of skin colour, seem to belong to a different racial group. These findings suggest that skin colour is not included in the top-down prior higher level body representations that constrain the experience of body ownership and that multisensory experiences might override ingroup/outgroup distinctions based on skin colour. This finding points to a novel possible role for sensory processing in social cognition. Maister and colleagues then followed up with the critical next step to ask whether changes brought about by multisensory integration can extend to the social processing of an entire social group (Maister et al., 2013) Light-skinned Caucasian participants experienced the rubber hand illusion over a dark-skinned hand, and the change in their implicit racial attitudes was measured using the Implicit Association Test (IAT). The experience of illusory ownership over the different-race hand was strongly correlated with increased implicit positive attitudes towards that race. Similar findings were subsequently reported using a virtual reality set-up in which participants embodied a different-race avatar. Again, changes in body ownership elicited by the RHI procedure lead to a decrease in implicit racial biases against the embodied racial group (Peck et al., 2013). Similar effects were reported for age-stereotypes (Banakou et al., 2013) and other higher order social and attitudinal processes such as autobiographical episodic memory (Bergouignan et al., 2014; Iriye & Ehrsson, 2022), self-concept (Tacikowski, Weijs, et al., 2020), gender identity (Tacikowski, Fust, et al., 2020), and self-compassion (Osimo et al., 2015).. Taken together, these findings demonstrate that changes in bodily self-awareness induced by multisensory stimulation can alter higher-level representations of the self and others such as social or racial stereotypes, as well as influencing low-level processes underlying social perception (Maister et al., 2015).

Our early experimental research also lead to a growing interest in experimental research into awareness of the developing body, including the sense of limb position and ownership in preverbal infants and children (Cowie et al., 2013, 2016; Filippetti et al., 2013; Filippetti & Crucianelli, 2019; Preston & Kirk, 2022; Rigato et al., 2014; Weijs et al., 2021; Zmyj et al., 2011). Important advances were made in understanding the developmental origins of the multisensory basis of limb representations. Whilst even newborn infants show some sense of visuotactile synchrony, the tuning of limb representations in action and perception undergoes significant change through the first year of life. During childhood, children are very highly susceptible to the rubber hand illusion. Specifically, a child's perceived hand position drifts towards the fake hand by three times as much as does an adult's hand. This effect, which reduces by 10-11 years, is thought to reflect visual capture rather than multisensory stimulation: the letter effect is important at all ages. As well as using bottom-up visuotactile and visuomotor information, children's hand localisation also depends on top-down information, since it is affected by the posture of the fake hand, along the lines shown in our 2005 paper. A more recent study (Weijs et al., 2024) looked at the sense of body ownership in participants ranging from 7 to 80 years using Virtual Reality and found that increasing multisensory asynchrony led to decreased measure of hand ownership across all the ages tested. In addition, sense of body ownership is increasing with increasing age independent of mismatch delay. The results suggest that as we age there is, at least partly, an enhanced weighting of top-down and a reduced weighting of bottom-up signals for the momentary sense of bodily self (see also (Marotta et al., 2018).

7. Models of the self

The RHI literature speaks in favour of an exteroceptive model of the self, within which self-awareness is highly malleable, subject to the perception of the body from the *outside*. However, exteroceptive input represents only one set of channels of information available for self-awareness. We are also *interoceptively* aware of our body. on the RHI's focus on exteroceptive multisensory signals such as vision and touch does not include an important additional dimension of embodiment

and self-awareness, namely, interoception. Interoception, as first suggested by Sherrington who coined the term in 1906 (Craig, 2009), is the body-to-brain axis of sensations originating from the body, and particularly from visceral organs that signal the body's physiological state. It can thus be distinguished from proprioception. More recent definitions ascribe interoception the role of both sensing and integrating all aspects of the body's physiological state and motivational needs, from low-level monitoring of blood chemistry, the representations of skin and body temperature and sensations evoked by affective interpersonal touch (Tsakiris & Critchley, 2016) . The impact of interoception therefore extends beyond homeostatic/allostatic reflexes and is fundamental to motivation, emotion (affective feelings and behaviours), social cognition and self-awareness (Seth & Tsakiris, 2018). A natural and important extension of research on body-ownership involved investigating how exteroceptive and interoceptive signals and representations might come together to give rise to a coherent awareness of one's own body, as perceived both from within and from the outside.

Moseley et al (2008) provided evidence that the experience of ownership during RHI is also accompanied by significant changes in the homeostatic regulation of the stimulated hand, in addition to changes in the subjective experience of one's body. In particular, skin temperature of the stimulated hand decreased if and when participants experienced the RHI (Moseley et al., 2008; Sadibolova & Longo, 2014). 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 occurred only as a result of the experience of ownership. Thus, a change in conscious experience of body-ownership has direct consequences for the physiological regulation of real body-parts that occur once participants experience the RHI, and not simply as the result of synchronous multisensory stimulation. However, this research area remains controversial. While further studies have reported similar effects (Tsakiris et al., 2011), failures to replicate skin temperature changes during the rubber hand illusion have also been reported (de Haan et al., 2017; Lang et al., 2021). In another study, histamine reactivity increased in the stimulated arm during the rubber hand illusion

(Barnsley et al., 2012), suggesting that interoceptive systems "disown" the affected at the same time as exteroceptive systems integrate the fake hand into the representation of the body. This effect recalls Damasio's definition of 'the self' as 'whatever the immune system defines as being part of the body' (Damasio, 2003). Other studies have shown that individuals with autoimmune diseases (Finotti & Costantini, 2016) and those with an overactive immune system (Finotti et al., 2018) experience a stronger and a weaker RHI respectively.

Beyond the purely physiological level, it was shown that both the experience of body-ownership, and subsequent changes in homeostatic regulation, depend partly on levels of interoceptive awareness. Participants with lower interoceptive awareness, indexed by a measure of interoceptive accuracy, experienced a stronger illusory sense of body-ownership during the RHI. The absence of accurate interoceptive representations might mean that one's model of self is predominantly exteroceptive (Tsakiris et al., 2011). This finding has been extended to the enfacement illusion (Tajadura-Jiménez & Tsakiris, 2014), has been replicated in children aged 8 to 17 years (Schauder et al., 2015) and has also been extended to a more mechanistic interoceptive framework that takes into account cardiac afferent signals occurring during systole (Moffatt et al., 2024). However, other studies have reported contrasting results (Horváth et al., 2020; Yamagata et al., 2023). Lastly, using another type of interoceptive stimulation, namely slow affective touch that activates CT afferents, Crucianelli and colleagues (2013) and van Stralen and colleagues (2014) demonstrated how this kind of stimulation enhances the experience of body-ownership in the RHI. Thus, integration of sensory information across interoceptive and exteroceptive pathways seems to change the awareness of one's own body and self. However, a more detailed mechanistic understanding of the interactions between interoception and exteroception requires improved interoceptive measures as well as better experimental control over the inputs to the interoceptive system, similar to the experimental control that we have over the inputs to the exteroceptive system.

8. Conclusion

A search for “Rubber hand illusion” returns 748 hits on Scopus (10/06/2024). More generally, interest in bodily sensation and bodily self-awareness has become central to psychology, particularly in the study of emotion and social cognition. In part this reflects the development of new experimental methods and measures that help to operationalise elusive theoretical constructs such as self-awareness.

The twenty years since publication of our paper have also produced a clearer computational framework for understanding bodily self-awareness, based on Bayesian models of causal inference and cue combination. These models have helped to provide testable predictions and a clearer understanding of the distinctions between current afferent input and prior representation in perceptual estimation.

While several theories of body-ownership, based on our neurocognitive understanding of the RHI, have been proposed over the years (Apps & Tsakiris, 2014; Blanke, 2012; Limanowski, 2022; Samad et al., 2015; Tsakiris, 2010) , they all converge on the suggestion that body-ownership is not a fixed mental representation of the body in the brain. Rather, it results from dynamic processes of multisensory integration, and integration of previously acquired “top-down” information or priors, and bottom-up afferent signals. The RHI is widely understood to be a perceptual illusion driven primarily by bottom-up multisensory signals, but modulated by a range of top-down factors ranging from prior cognitive models of one’s body structure (Tsakiris, 2010) to individual traits such as sensory suggestibility (David et al., 2014; Marotta et al., 2016) and phenomenological control (Lush et al., 2020). Functional neuroimaging studies using the RHI and related paradigms have accordingly shown that body-ownership is supported by a network of multimodal areas, composed of premotor, temporoparietal, and occipital areas, the insular cortex and the posterior parietal cortex as well as subcortical areas such as the putamen and the cerebellum (Brozzoli et al., 2012; Chancel, Iriye, et al., 2022; Ehrsson et al., 2004; Limanowski et al., 2014; Limanowski & Blankenburg, 2016; Tsakiris et al.,

2007, 2008; Tsakiris, Longo, et al., 2010). General computational frameworks for brain science have developed theoretical (Apps & Tsakiris, 2014; Fotopoulou, 2015; Limanowski & Blankenburg, 2013) and computational (Bertoni et al., 2023; Chancel, Ehrsson, et al., 2022; Fang et al., 2019; Samad et al., 2015) interpretations of the RHI paradigm. These suggest mechanisms by which afferent sensory signals and prior beliefs converge to give rise to body-ownership as a consequence of probabilistic inferences of the most likely cause of one's multisensory experience in a given context**.**

Enduring dualistic conceptions have tended to encourage psychologists to treat self-awareness and self-concept as a pure product of mind, and ignore the role of the body. If the self is considered primarily in terms of episodic memory, or self-concept and self-appraisal, this tendency may seem justified. Nevertheless, "all over the world, self begins with body" as Roy Baumeister (1999) has noted. A main message emerging from our work, which we have updated and highlighted in this piece, is the cognitive importance of representing oneself as a physical object, as one's physical body. This object is unusual, because its sentience and agency are directly experienced. In contrast, sentience and agency are rare for other types of objects and can only ever be inferred.

Decades after the publication of the first report on the RHI and our subsequent paper that revisited this illusion, the field continues to advance our understanding of body-ownership but also to debate. A recent study (Lush et al., 2020) argued that the RHI arises, at least partially from hypnotic suggestibility. Lush and colleagues offer a cognitive interpretation of the RHI that, they claim, radically departs from the generally accepted conception of the RHI. The general influence of top-down factors for the RHI was already made clear by the discussion of beliefs about one's own body in our original paper. Lush and colleagues focus instead on the role of beliefs about the likely experiential consequences of the experimental situation. Beyond the issues relating to the robustness and interpretation of their data (Ehrsson et al., 2022), a broader issue relates to the very nature of our embodiment.

We might think of the experience during the RHI as an instance of how people experience their own bodies in everyday life. That this experience comes by degrees, and that there are individual differences should not come as a surprise. People differ in how embodied they are, how much attention they pay to different sensory modalities, how precise are different sensory priors and prediction errors and how differently they are weighted. Iris Murdoch wrote in her novel 'The Severed Head' : "Yes, some people *are* more their body than others". The basic mechanisms of embodiment are comparable across individuals, as the literature on bodily illusions suggests, but the weighting of different sensory signals (Apps & Tsakiris, 2014) , the fine-tuning of multisensory integration (Chancel, Ehrsson, et al., 2022; Costantini et al., 2016), the strength of interoceptive processing (Ainley et al., 2016) influence how individuals experience embodiment. Personality traits (Lush et al., 2020) and intersubjective relations may influence how somatic signals are mentalized (Fotopoulou & Tsakiris, 2017) and culture may additionally have effects (Pelkey, 2023). Thus, there are individual differences in embodiment experience, as there are individual differences in awareness of other signals. There are also individual differences in metacognition of such signals, and of course individual differences in somatization, body-image concerns, self-recognition and so on. The RHI, as an experimental model of embodiment, makes this variability scientifically accessible. The research inspired by Botvinick and Cohen's original paper have succeeded in advancing our neurocognitive understanding of one of the most fundamental experiences of the human condition, namely the sense of being one's body, and of the richness and complexities of this experience. There is much more research to be done in the next twenty years and we look forward to it.

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