The bodily self: Insights from clinical and experimental research

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Review

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ABSTRACT

This review article summarizes neuropsychological descriptions of abnormal body representations in brain-damaged patients and recent neuroscientific investigations of their sensorimotor underpinnings in healthy participants. The first part of the article describes unilateral disorders of the bodily self, such as asomatognosia, feelings of amputation, supernumerary phantom limbs and somatoparaphrenia, as well as descriptions of non-lateralized disorders of the bodily self, including Alice in Wonderland syndrome and autoscopic hallucinations. Because the sensorimotor mechanisms of these disorders are unclear, we focus on clinical descriptions and insist on the importance of reporting clinical cases to better understand the full range of bodily disorders encountered in neurological diseases. The second part of the article presents the advantages of merging neuroscientific approaches of the bodily self with immersive virtual reality, robotics and neuroprosthetics to foster the understanding of the multisensory, motor and neural mechanisms of bodily representations.

1. Introduction

In this review article, we present an overview of clinical and experimental approaches to the study of body representations (also called body schema, corporeal awareness or bodily self), providing insight into their neural and cognitive bases.

The first section provides an overview of unilateral and non-lateralized neurological disorders of the bodily self, often following damage to the right cerebral hemisphere. Here, we address hemiasomatognosia, feelings of disappearance and transformation of body parts, supernumerary phantom limbs, somatoparaphrenia and autoscopic phenomena involving the entire body. Disorders of the bodily self have been difficult to classify systematically, as noted historically by pioneering researchers [1–5] and in more recent works [6–8]. Indeed, the bodily self is in itself a conceptually complex topic, because its experience is inherently multimodal, subjective, and global. The bodily self arises from the dynamic integration of bodily and environmental visual, tactile, proprioceptive, vestibular, auditory, olfactory, visceral and motor information [9]. Unlike other worldly objects, the body is the source of its own perception, a subject and an object at the same time. The human brain computes bodily information via different maps and networks, notably areas of tactile, proprioceptive, vestibular and interoceptive projection in the primary somatosensory, as well as unimodal and heteromodal cortices, providing an unified and global representation of the lived body, which allows for experiencing it as a unique self and agent. To these sensory components, recent research has added spatial and social factors involved in self-other bodily interactions, and ego- and altercentric perspectives on bodily and action perceptions [10,11].

Verbal and higher-level cognitive aspects of bodily knowledge are sometimes subsumed under the concept of "body image," said to be a conscious and abstract representation of the body, involving for instance the naming of body parts and general knowledge about human bodies. This classical distinction with "body schema," which involves situated, directly experienced, unconscious, and non-verbal aspects of the bodily self has been widely discussed elsewhere (e.g., [12,13]), and we adopt the view here that asomatognosia per se pertains to the body schema domain [14,15]. As such, we think that disorders such as autotopoagnosia (impaired naming and pointing of body parts on demand [16,17]), Gerstmann's syndrome (among other symptoms, impaired naming and pointing of fingers on demand [18,19]), or ideomotor apraxia (impaired production of goal-directed gestures on demand [20]) – all involving damage to the left parietal lobe – are clinically, phenomenologically and conceptually different from disorders of

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the body schema and will not be addressed here. Thus, this review focuses on disorders of the body schema, which are predominant after right brain damage [21].

In the second section, we summarize current experimental investigations in healthy subjects regarding the bodily self. We focus on experimental paradigms that have created multisensory conflicts (often involving visual and tactile signals) to modulate the body schema (e.g., evoking a virtual Alice in Wonderland syndrome [22] or the sense of having a child body [23]), the sense of owning the body (e.g., evoking the rubber hand illusion [24]), and the sense of embodied self-location (e.g., evoking an out-of-body–like illusion [25]). These approaches have been found promising to better understand the sensorimotor mechanisms that underlie a large range of bodily disorders observed following brain damage or during epileptic seizures or migraine episodes (Table 1).

Finally, we offer some concluding remarks highlighting the importance of merging approaches from neuropsychology with modern neuroimaging techniques and protocols from cognitive neuroscience, immersive virtual reality, robotics and neuroprosthetics for establishing a more comprehensive model of the human bodily self and its disorders.

2. Disorders of the bodily self

2.1. Unilateral disorders of the bodily self

2.1.1. Hemiasomatognosia

The term "hemiasomatognosia" was coined by French neurologist Jean Lhermitte [3] to refer to a neglect, lack of interest, or unawareness of one part or entire half of one's body. Such patients generally ignore their left arm and/or leg; they behave and speak as if these did not exist. One of Zingerle's [26] patients, with left hemiplegia, did not pay the slightest attention to his left side, never looked at it, never spoke about it. All orders to move were executed on the right side, and, when confronted directly, the patient did not see any absurdity in having only one body side. Zingerle and Lhermitte saw in this profound unawareness for one body side the source of other clinical phenomena such as anosognosia and unilateral neglect. In the French clinical literature, notions such as unawareness (*méconnaissance*) and lack of ownership (*désappartenance*) were later often used to describe hemiasomatognosia's diverse manifestations. Frederiks [27] attempted to clarify the issue by proposing a distinction between "conscious" and "non-conscious" hemiasomatognosia. The former referred to patients who perceived their body as incomplete or amputated, yet fully realized the illusory nature of these feelings. The latter referred to the subjective "disappearance" of one half of the body (most often the left one), without the patient being able to notice this very disappearance. Today, "non-conscious hemiasomatognosia" is conceived of as personal neglect, motor neglect, or anosognosia for hemiplegia. In each of these cases, there is some kind of indifference for a body part. Personal neglect refers to the classical picture of a patient who "forgets" to comb, shave or make up the left side because of an attentional, perceptive or representational disorder. Motor neglect refers to patients without objective motor disorders who underutilize their left members [1,28]. These patients behave as if they were hemiplegic although they are not. Conversely, patients with anosognosia for hemiplegia behave as if they are not paralysed: importantly, they not only deny that they are paralysed, they also tend to ignore their left side in general. Frederiks [27] summarized these symptoms as "attentional disorders for the hemibody". Garçin et al. [29] wrote of a particularly striking case: "The observer gets the feeling that the subject behaves as if he underwent an amputation of the left side of the body". The loss of lateralized body part representations can occur at different levels of multisensory, sensorimotor or cognitive integration. For instance, patients may recognize their own body parts when presented visually but completely forget about them when they are out of sight.

2.1.2. Feelings of amputation, hemi-depersonalization

Here we address disorders labelled "conscious hemiasomatognosia" by Frederiks [27]. Such patients have vivid feelings that a part of their body has disappeared or feel it strongly diminished or blurred. Conceptually, these disorders seem to be the reverse of phantom limbs after amputation (most amputees retain a sensation of completeness despite having physically lost a body part). In both cases, patients fully appreciate the illusory nature of their sensations.

A related disorder is the feeling that a body part is no longer attached to the rest of the body, as if it were "floating" at some distance (sensation of disconnection or splitting). Symptoms of absence or separation of body parts are usually of short duration and appear mostly as part of seizures or migraine episodes [2,4,27,30]. Other cases occur due to cortical or subcortical strokes [31]. Direct electrical stimulation at the right temporo-parietal junction can also induce this type of illusion in the visual modality [32]. These symptoms are not necessarily accompanied by hemiplegia, unilateral neglect or anosognosia. Sometimes, a sensation of strangeness for an "absent" or "disconnected" body part, then felt as "alien", "numb" or "empty", is reported: the term hemi-depersonalization, or depersonalization for a body part, has been suggested [1,3]. Patients with such symptoms often feel the need to control these body parts by sight or touch, without such strategies being always able to restore normal bodily feelings [1].

Other symptoms can involve distortions in the perceived size of selected body parts or half of the body. These subjective alterations of bodily size are vividly experienced but are usually recognized as illusory. To refer to these symptoms, Frederiks [33] used the terms microsomatognosia and macrosomatognosia. Both terms are reminiscent of the concepts of *hyposchématie* (i.e., a shrinking of the body representation) and *hyperschématie* (i.e., an enlargement

Table 1
Main models for neuropsychological, neuroscientific and neuroimaging investigations of the body schema/image and the sense of body ownership and self-location/embodiment.

Bodily experience	Clinical (neuropsychological) model	Experimental (neuroscientific) model	Functional neuroimaging model
Body schema/body image	Macro/microsomatognosia [33] Supernumerary phantoms [44] Anorexia, bulimia nervosa Body identity integrity disorder [108]	Rubber hand illusion [24] Immersive virtual reality [22,23,104]	Shrinking illusion [109]
Body ownership	Somatoparaphrenia [50] Body identity integrity disorder [108]	Rubber hand illusion [24] Virtual arm illusion [81] Numbness illusion [84]	Rubber hand illusion [85,87] Virtual arm illusion [110]
Self-location/embodiment	Autoscopic hallucinations: out-of-body experience [67] Heautoscopy [74]	Full-body illusion [92] Out-of-body illusion [25] Body swap illusion [98] Immersive virtual reality [103]	Full-body illusion [76] Body swap illusion [86]

of the body representation) originally coined by Bonnier [34] in 1905 to describe distortions of the body schema (*aschématie*) in patients with sensory and central disorders [35]. In neurology, microsomatognosia (*hyposchématie*) occurs when a body part is experienced as smaller than usual (e.g., some hemiplegic patients perceive their hand as a child's hand). In macrosomatognosia (*hyperschématie*), a body part is perceived as larger than usual, oftentimes much heavier too. The illusion can expand to such degrees that the body part is felt as filling the room or hitting the roof. These disorders occur most often during migraine [36] or epileptic seizures [2] but also after brain damage leading to sensory or motor impairment [33,37].

2.1.3. Supernumerary phantom limbs

"Supernumerary phantom limbs" refer to the subjective experience of having an additional body part, usually a limb, felt as an entity sharing properties with a physical body counterpart and occupying a different place in space. Some patients experience the presence of a "third limb" and clearly identify this experience as an illusion, whereas others report multiple arm or leg reduplications as part of a delusion and seemingly believe in their physical existence [38–40]. In the latter case, the term "delusional reduplication of parts of the body" has been applied [39]. Supernumerary phantom limbs have been scarcely reported in the literature [40–42], yet they display striking diversity in their manifestations. In most cases, the "additional limb" is a static somesthetic percept located separately, but on the same side, of a plegic limb. It is sometimes felt as smaller and in different, or even awkward, positions, than the physical counterpart limb.

Movements of the supernumerary phantom are rather rare and most often automatic or involuntary (see Fig. 1 and [42]). A woman with right fronto-mesial damage involving the supplementary motor area and the cingular gyrus and no hemiplegia or motor disorders reported the following peculiarity: whenever she moved her physical limb, a phantom seemed to occupy, after a few seconds, the place left by the real limb [43]. Thus, the existence of this supernumerary phantom specifically relied on movements of the real counterpart limb. Still another patient reported not only being able to "trigger" and move her supernumerary phantom voluntarily but also claimed to see it (as somewhat whitish and transparent) and sometimes even felt it touch her face. In addition, this complex phantom, as reported by the patient, could not coexist in the same place with other objects or body parts (in which cases it "disappeared" instantly) [44]. Such a clinical presentation is rare but neatly illustrates the diversity of supernumerary phantom limbs in terms of the involved modalities, motor aspects and sensitivity to feedback. This diversity is also reflected in the involved brain areas: most often, the right hemisphere is implicated, but the basal ganglia, parietal lobe, thalamus, medial prefrontal cortex or supplementary motor area can also be involved [15].

2.1.4. Somatoparaphrenia

Gerstmann [45] coined the term "somatoparaphrenia" to refer to clearly delusional disorders of the bodily self. According to this author, some related cases deserved to be distinguished according to the mental frame of the patients. Most patients with hemiasomatognosia and anosognosia for hemiplegia remain indifferent or make rather limited claims regarding their impairment, whereas others seem to "stand apart" by virtue of their sheer bizarreness and exuberance. Here, is Gerstmann's original definition of somatoprahrenia: "[A] specific psychic elaboration (marked by formation of illusions, confabulations and delusions) with respect to the affected members or side of the body, believed or experienced as absent" (p. 912). Somewhat confusingly, the term "verbal asomatognosia" has also been used

Fig. 1. Supernumerary phantoms. A 37-year-old woman reported the sensation of having a third left arm and less frequently reported the sensation of having a third left leg. The patient had no voluntary control of the phantom limb movement, but the phantom followed the motion of the real left hand. The patient was fully aware of the illusory nature of her experience, although the phantom limbs felt so vivid that she had difficulties distinguishing them from the physical limbs. MRI revealed an infarction of the right dorsomedial frontal lobe as well as prenatal lesion of the corpus callosum. Note that the patient's drawing is mirror-reversed so that she represented her left body on the right side of the image.
Reproduced from Hari et al. [42] Three hands: fragmentation of human bodily awareness. *Neurosci Lett* 1998;240(3):131–4, with permission from Elsevier.

to refer to cases in which patients misidentify their own left hand, presented visually by the experimenter for someone else's hand [46]. Somatoparaphrenia is mostly used to refer to false beliefs regarding one's body part or half body, the most frequently reported being the belief that they belong to someone else. To that extent, current and classical definitions of delusional disorders directly apply to somatoparaphrenia [47–49]. However, as with supernumerary phantom limbs, the clinical presentation of somatoparaphrenia differs considerably among patients, which suggests different types of somatoparaphrenia.

The most common type of somatoparaphrenia is the misattribution of one's body part (usually the left hand, arm or leg) to the doctor, a nurse, a neighbouring patient, or someone unspecified [26,45,50]. Some patients also misattribute their paralysed limb to someone absent or even long dead [51]. A sophisticated and delusional account of the event can be provided, oftentimes with a persecutory flavour. For instance, a patient reported by Hécaen et al. [52], went to the length of complaining by letter to a nurse she accused of having taken away her arm and threateningly asked her to bring it back. The intensity of the delusion can vary: some patients acknowledge that their claims are bizarre, and others steadfastly hold onto their beliefs. By closely inspecting the arm from the shoulder down, patients can come to realize that it belongs to them, but not always [51]. One patient thus declared: "my eyes and my feelings don't agree, and I must believe my feelings. I know they look like mine [the affected limbs], but I can feel they are not, and I can't believe my eyes" [5].

One patient reported by Hécaen and de Ajuriaguerra provides a good illustration of how difficult it is sometimes to categorize these disorders [2]. This patient spontaneously denied that his left hand belonged to him but did not attribute it to someone else (when shown his hand, he simply said "it's not mine"). However, upon seeing the doctor's hand, he claimed he recognized his hand ("there is mine"). The patient held to this idea even when the doctor produced movements with his hand and took a few steps back. He began to doubt his assertion only when the doctor was too far away ("I'm starting to believe that it is not mine"). Thus, there are 2 types of ownership misattribution in somatoparaphrenia: some patients identify their limb as from another person (self-as-other error), while others identify another person's limb as their own (other-as-self error, this type being much more rarely reported).

Brain damage leading to somatoparaphrenia involves a wide fronto-temporo-parietal network in the right hemisphere and more specifically the insula, the prefrontal and orbitary cortex, the underlying white matter and subcortical structures (thalamus, basal ganglia and amygdala) [50,53–55] as well as the hippocampus [15]. The implication of multisensory regions in the abnormal sense of owning a body suggests that coherent multisensory integration is required for elaborating bodily self-consciousness. Somatoparaphrenia, like many other alterations of bodily self-consciousness [9], may in part be related to misintegration of or conflicts between proprioceptive, interoceptive and vestibular signals about one's body position and motion with visual signals from the body. Interestingly, sensory signals modulation by caloric vestibular stimulation [56–58] and visual inspection of the disowned hand in a mirror [59] can significantly decrease somatoparaphrenic delusions. Therefore, body ownership is under the control of peripheral sensory signals.

2.2. Non-lateralized and bilateral disorders of the bodily self

The previous section provided an overview of lateralized (mostly on the left side) disorders of the bodily self. Here, we briefly address non-specifically lateralized disorders and disorders extending to the entire body. For instance, macrosomatognosia can sometimes involve the head or the entire body, inducing feelings of enormity or of "filling the room". This kind of symptom occurs mostly during migraine auras and are called Alice in Wonderland syndrome [60]. Other patients can feel their entire body as absent or unreal, typically during depersonalization [61] or, in more extreme cases, describe their body as dead or non-existent, a condition called Cotard syndrome (which Lhermitte termed "total asomatognosia" [3]). More generally, such symptoms and those that follow can be conceptualized as "complete" forms of the unilateral disorders reviewed in the previous sections [62–64].

The most striking disorders involving the misrepresentation of the entire body are those sometimes labelled "illusory doubles", reminiscent of the "delusional reduplication of body parts" described above, and of the "double" and *doppelgänger* motives in romantic and gothic literature [65]. Such striking alterations of the global bodily self occur under varied circumstances, not necessarily pathological, and are most often transitory. They are currently described and studied under the term "autoscopic phenomena" [66–68]. This area includes multimodal illusions producing more or less complete doubles of the body. Subjects can thus perceive a visual projection of their own body in front of them (autoscopic hallucination), in which case the "double" appears as a mirror reflection in external space, while the real self remains firmly tight to its physical body and location. Therefore, autoscopy as such is mainly a visual phenomenon, although it can sometimes involve some motor resonance when the double moves according to the subject's own movements.

In other cases, the subject reports feeling the location of the "self" at the same time in the projected double and in the physical body (heautoscopy) or alternating between them. The "double" can then acquire some limited sensorimotor and psychological autonomy and is thus close to the literary *doppelgänger* described by Hoffmann, Dostoyevsky, Poe and Hogg. Heautoscopy has a visual component but also involves unstable vestibular and sensorimotor aspects [67,69] and a strong emotional affinity (or repulsion) towards the "double". When the double is not actually seen but rather felt in close spatial proximity, the condition is called "feeling of a presence." The subject has a more or less fleeting sensation of someone's presence nearby, without being able to clearly perceive or identify it but also without experiencing it as a double of oneself [70].

When the perspective of the subject is entirely relocalized in the projected double and thus the subject has the vivid sensation of being "out-of-the-body" and can "see" the physical body from a distant and elevated perspective, the condition is called "out-of-body experience" [32,67,68]. During such episodes, widely popularized by their inclusion in the hallucinatory phenomena called "near-death experience" [71], there is a very strong vestibular involvement (feelings of lightness and floating, reversal of the visuo-spatial perspective), and the purely autoscopic component ("seeing oneself") can be less prominent or altogether absent [69,72,73].

In neurological cases, autoscopic hallucination, being mostly visual disturbances, involves damage to the occipital cortex, often unilaterally [74]. Other disorders, being more complex, involve varied disturbances of multimodal and vestibular integration, notably at the left posterior insula regarding heautoscopy [74], the insula and a fronto-temporo-parietal network for the feeling of a presence [75], and the right temporo-parietal junction for out-of-body experiences [76].

In the next section, we describe experimental procedures developed to study mechanisms underlying the bodily self in healthy subjects, to better understand the disorders we have described.

3. Neuroscientific investigations in healthy participants

In this section, we summarize recent work from neuroscience and experimental psychology that has endeavoured to investigate how the brain represents some aspects of the body and the self. We focus on research of healthy participants related to the sense of owning the body (altered in somatoparaphrenic patients) and self-location/embodiment (altered during out-of-body experiences) (see Table 1), 2 experiences deemed crucial for establishing a minimal sense of selfhood [77].

3.1. Investigating body part representations

Healthy participants research has extensively used the "rubber hand illusion" (RHI) [24,78] to investigate the multisensory foundations of body ownership as well as its neural underpinnings

(Fig. 2A). The RHI is evoked when a rubber hand placed in the participant's field of view is touched in synchrony with the participant's hand (hidden to the participant). After a minute of synchronous stimulation of the fake and real hands, some participants report that the rubber hand feels as if it were their own hand. Subjective reports measured by questionnaires (i.e., visual analog scales) indicate that illusory ownership for the rubber hand is significantly larger for synchronous than asynchronous visuo-tactile stroking. In addition, the RHI is characterized by a mislocalization of the participant's hand in space. When asked to locate their hand in the horizontal plane (e.g., by pointing with their right hand toward the tip of their left index finger), participants tend to locate their hand closer to the rubber hand than it actually is. This error in self-hand localization towards the rubber hand has been termed "proprioceptive drift" and is classically interpreted as a consequence of a "visual capture" [79,80].

Several variants of the RHI developed include presentation of a virtual hand in immersive virtual environments (i.e., the "virtual arm illusion" [81]; see Fig. 2B), or the presentation of multiple hands [82]. Ehrsson et al. [83] developed a variant of the RHI during which the experimenter uses the participant's right index finger to touch a left rubber hand while the experimenter touches the participant's left hand with the experimenter's own finger (Fig. 2C). This procedure creates the sensation that participants are touching their own hand (instead of a rubber hand) with their right index finger. Another paradigm, the "numbness illusion" [84], replaces the rubber hand by a confederate's hand. In this illusion, the participant and the confederate have the palm of their hands pressed against each other. Participants stroke their own left index finger using their right thumb and at the same time stroke with their right index finger the confederate's index finger (Fig. 2D). Participants may experience their left index as numb (hence the term "numbness illusion") or bigger, as if it were encompassing the confederate's index finger. These sensations occur only when the participant's and confederate's index fingers are synchronously stroked.

Several neuroimaging studies investigated the neural underpinnings of body part ownership by using the RHI. Brain areas significantly more activated during the RHI (i.e., during synchronous visuo-tactile stimulation) were mostly located in the insula, cingulate cortex, premotor cortex and extrastriate cortex (extrastriate body area, EBA) [83,85,86]. Moreover, an increase in the BOLD signal in the insula was positively correlated with the magnitude of the proprioceptive drift [87]. Finally, one study [84] recorded somatosensory evoked potentials during the numbness illusion while participants received electrical stimulation of the median nerve. The numbness illusion was associated with increased amplitude of the N20 component of somatosensory evoked potentials. This result suggests somatosensory enhancement in the primary somatosensory cortex, in keeping with increased evoked potentials over the somatosensory cortex reported after real anaesthesia of the participant's hand [88].

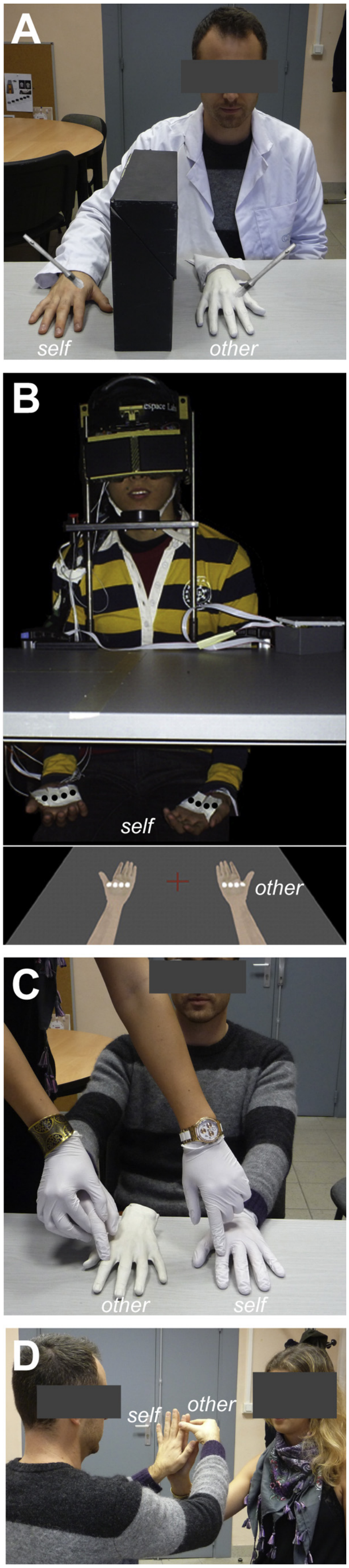

Fig. 2. Paradigms to investigate ownership for body parts. A. In the visual variant of the "rubber hand illusion," the experimenter uses 2 identical paintbrushes to synchronously or asynchronously stroke the participant's hand (not visible to the participant) and a realistic rubber hand (visible to the participant). B. In the "virtual arm illusion," spatial and temporal synchrony is created between the touch applied to the participant's hand (top part of the figure) and the touch observed on the virtual arm (bottom part of the figure: scene shown in the head-mounted display). Reproduced from Evans and Blanke [110]. Shared electrophysiology mechanisms of body ownership and motor imagery. *Neuroimage* 2013;64:216–28. http://dx.doi.org/10.1016/j.neuroimage.2012.09.027, with permission from Elsevier. C. In the non-visual variant of the rubber hand illusion, spatial and temporal synchrony is created between the touch applied to the rubber hand by the participant's right index finger (that is passively moved by the experimenter) and the touch applied by the experimenter to the participant's left hand. D. In the "numbness illusion," the participant (here on the left part of the picture) strokes with his right thumb the dorsal part of his left index finger and at the same time strokes with his right index finger the dorsal part of the confederate's right index finger.

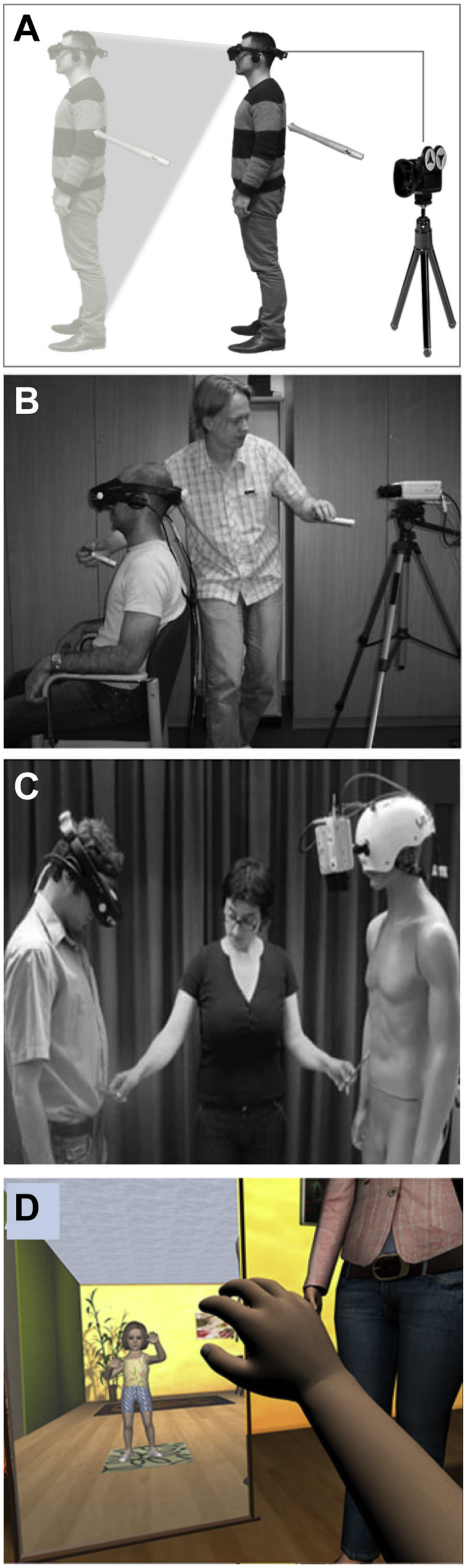

Fig. 3. Experimental paradigms to investigate whole-body ownership and self-location. A. Paradigm used to evoke the "full-body illusion": identification with the body seen in the head-mounted display and apparent forward shift in self-location. B. Paradigm used to evoke the "out-of-body illusion": identification with the body seen in the head-mounted display and apparent backward shift in self-location. Reproduced from Ehrsson [25]. The experimental induction of out-of-body experiences. *Science* 2007;317:1048, with permission from The American Association for the Advancement of Science. C. Paradigm used to evoke self-identification with a plastic mannequin's body without change in self-location. Reproduced from Petkova and Ehrsson [98]. If I were you: perceptual illusion of body swapping. *PLoS One* 2008;3:e3832. http://dx.doi.org/10.1371/journal.pone.0003832. D. Immersive virtual environment coupled with motion tracking systems to induce self-identification with a child avatar seen in a head-mounted display. Reproduced from Banakou et al. [23] Illusory ownership of a virtual child body causes overestimation of object sizes and implicit attitude changes. *Proc Natl Acad Sciences U S A* 2013;110(31):12846–51. http://dx.doi.org/10.1073/pnas.1306779110.

We conclude this section by emphasizing recent findings showing that illusory ownership over a fake hand changes several aspects of the own body physiological states [89,90]. For example, Moseley et al. [90] reported that illusory ownership of a right rubber hand significantly reduced the temperature recorded over the participant's right hand. This temperature reduction was not found for the participant's left hand and foot (not stimulated during the experiment), so disrupting the sense of ownership for a given body part modifies temperature regulation at the level of this same body part. Interestingly, body ownership abnormalities and change in temperature regulation are associated in several clinical conditions such as schizophrenia, neuropathic pain, anorexia and bulimia nervosa [90]. Thus, the relation between body ownership/disownership and homeostatic regulation may shed light on the multisensory mechanisms of several conditions characterized by abnormal body representations.

3.2. Investigating whole-body representations

Investigating the RHI and related illusions would not be enough to understand the sensorimotor foundations of human bodily self-consciousness because it addresses only body part representations. Yet, in addition to representations of multiple body parts, and perhaps more importantly, the bodily self, also entails global and coherent whole-body representation [9,77]. Accordingly, recent neuroscientific investigations into the bodily self have endeavoured to adapt the RHI to the entire body by using the same principles, that is, visuo-tactile or visuo-motor synchrony between the physical body and the seen (fake) body [91].

In the "full-body illusion" [92], participants wore a head-mounted display through which real-time videos of their own body can be seen from the back (the video recording system being placed a couple of meters behind their own body), or videos of a plastic mannequin or a virtual character [92–96]. Thus, participants standing upright observed their own body (or the mannequin's body) as if it was seen from an external, third-person perspective (i.e., as if participants were located some meters behind this body) (Fig. 3A). When a tactile stimulation was applied on the participant's back, in synchrony with touch applied to the back of the body depicted through the head-mounted display, participants self-identified with this body. Self-identification (measured by using questionnaires) was significantly stronger after synchronous than asynchronous visuo-tactile stroking. As for the RHI, self-identification with the avatar decreased skin temperature at the level of the participant's body [97] and reduced the participant's pain perception [95]. In addition, the full-body illusion was characterized by errors in self-localization in space. Fig. 4 illustrates the procedures for measuring a "whole-body" proprioceptive drift and shows that participants localized themselves closer to the observed body after they received synchronous visuo-tactile stroking. Across several variants of the illusion, the mean proprioceptive drift was 17 ± 7 cm for visuo-tactile stroking and 3 ± 6 cm for asynchronous stroking, which differed significantly

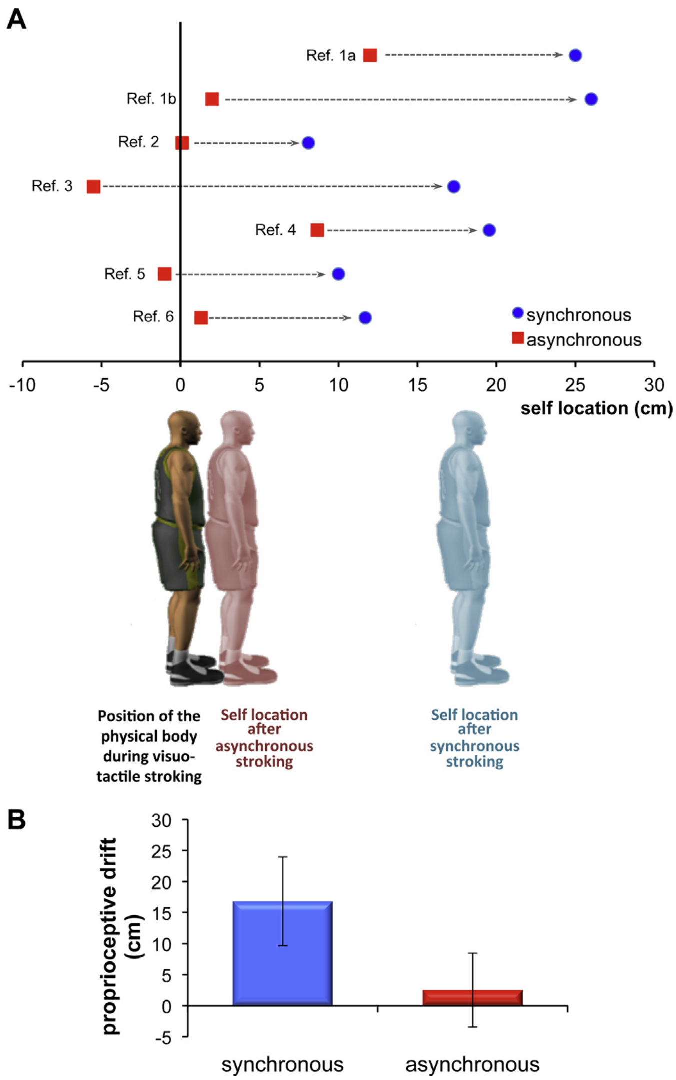

Fig. 4. Illusory self-location evoked during the full-body illusion. After a period of synchronous or asynchronous visuo-tactile stimulation, participants were displaced backwards and asked to walk back to where they thought they were located during the experiment. The position where participants stopped was taken as a measure of self-location in the horizontal space during the full-body illusion. This procedure was conducted to measure a "whole-body" proprioceptive drift, similar to that measured with the rubber hand illusion. A. Participants walked significantly further towards the seen avatar after synchronous visuo-tactile stroking (blue symbols) than after asynchronous visuo-tactile stroking (red symbols). The zero position indicates the location of the participant's body during the visuo-tactile stroking and positive and negative values indicate drifts of self-location towards and away from the seen avatar, respectively. Data are plotted according to ref. 1a and 1b [92], ref. 2 [94], ref. 3 [96], ref. 4 [95], ref. 5 [111], and ref. 6 [112]. Reproduced from Lopez et al. [11] In the presence of others: self-location, balance control and vestibular processing. *Neurophysiol Clin* 2015;45(4–5):241–54. http://dx.doi.org/10.1016/j.neucli.2015.09.001. Copyright 2015 Elsevier Masson SAS. All rights reserved. B. Data are mean ± SD proprioceptive drift calculated across several variants of the full-body illusion.

($P < 0.005$) [11]. Because the magnitude of this drift is rather small, as for the proprioceptive drift observed during the RHI, it can be seen as a compromise between the physical self-location and a full-blown disembodied self-location at the position of the avatar the participants self-identified with.

A variant of the full-body illusion is referred to as the "out-of-body illusion" [25] (Fig. 3B). In contrast with the full-body illusion, participants were stroked on their chest while they observed in a head-mounted display a real-time video of their own body seen from the back. Self-reports included statements such as "Wow! I felt as though I was outside my body and looking at myself from the back" [25]. Self-identification with the seen body was measured by recording skin conductance responses while participants observed a threat directed towards the seen body. The skin conductance response was larger after synchronous than asynchronous visuo-tactile stroking. In another variant of the illusion, participants bent their head forward as if they were looking at their own stomach and feet [86,98,99] (Fig. 3C). They wore a head-mounted display in which videos of a plastic mannequin were shown from an elevated viewpoint. In contrast with the full-body illusion and the out-of-body illusion, the mannequin was seen from a first-person perspective (but seen from a disembodied, third-person viewpoint in the former illusions) and with a descending viewpoint. Participants and the mannequin received either synchronous or asynchronous visuo-tactile stroking, and the degree of identification with the mannequin was measured both subjectively (questionnaires) and objectively (skin conductance response). Synchronous visuo-tactile stroking evoked stronger self-identification with the mannequin and stronger emotional responses when participants observed a threat directed towards the mannequin's stomach.

Only a few functional MRI studies have analysed brain activity during the body illusions described above. The "full-body illusion" modulates the BOLD signal at the temporo-parietal junction, in close vicinity of areas that are most frequently damaged in patients reporting out-of-body experiences [76]. In contrast, observing from a first-person perspective a mannequin's body being touched in synchrony with one's body activated mostly the premotor cortex but not the temporo-parietal junction [100].

Finally, it is notable that immersive virtual environments and motion capture technologies have fostered investigations of the multisensory foundations of body representations because they allow presenting realistic human avatars and manipulating their shape, size, age and skin colour [22,101–104]. A general outcome of these virtual reality studies was that spatio-temporal synchrony between the participant's motion and that of an avatar embedded in a virtual environment led participants to strongly self-identify with the avatar. Recent studies indicate that sensorimotor synchrony between the physical and virtual body not only modulates the participants' own body representation but also alters aspects of their affective and moral judgments. For example, synchronous motion between the participant and an avatar depicting a 4-year-old child modified the participant's body schema, as measured by their ability to manipulate virtual objects [23] (Fig. 3D). In this study, participants overestimated the size of objects after they identified with a 4-year-old child avatar. In the same line of research, self-identification with an overweight avatar changed the perceived size of the participant's body and their potential actions in the environment [104]. Several therapeutic interventions in neurology and psychiatry have recently been derived from immersive virtual environments given the apparent ease to induce self-identification with avatars and to modulate bodily, social and affective representations by using appropriate technologies [101,105].

4. Conclusions and clinical outcomes

Clinical cases and recent neuroscientific studies summarized in this review indicate that representations of the body and self are varied, multimodal and plastic. Regarding clinical cases, one fact must be highlighted: our current understanding of the bodily self historically mostly depends on careful examination of a wide array of clinical conditions. As a private and subjective experience, the bodily self and its disturbances can only be approached through systematic and empathic questioning of patients willing to share their feelings and sensations. To further investigate this topic, investigators and clinicians must know their semiology and pursue this purely clinical endeavour. Even in this day and age of new neuroimaging technologies, data analysis methods and virtual reality settings, patients and their stories remain the most precious avenue to discover more about our sense of bodily awareness and ownership. When possible, the clinical exam should involve a full neurological, neuropsychological, psychiatric and neuroimaging investigation. The interview should let patients speak by themselves, describe their bodily feelings in their own words, and then focus on more detailed aspects, such as those described in the section "Disorders of the bodily self" of this article [6]. Some questionnaires and guidelines have been published [6,106,107]. It is highly unlikely that all disorders of the bodily self have been discovered, described and labelled: we thus insist that clinical investigation, case reports and case series are still an absolutely necessary approach for the study of the bodily self.

However, as we have seen, experimental research can exploit multiple methods and paradigms to further investigate neural, cognitive, affective, spatial and social correlates of bodily awareness. Virtual reality, robotics, neuroprosthetics and increasingly other methods will certainly help delineate the mechanisms for multisensory and cerebral bodily representations. Such studies have already revealed the highly plastic nature of the bodily self, sensitive as it is to rather simple visuo-tactile and visuo-motor conflicts. From these results, these experimental methods now seem to be very promising non-invasive approaches toward rehabilitation of patients with neurologic and psychiatric disorders.

Disclosure of interest

The authors declare that they have no competing interest.

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