

Title of the chapter: Representation and perception of the body in space

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15 Keywords (alphabetical order):

1. bodily self
2. body image
3. body memory
4. body model
5. body representations
6. body schema
7. body semantics
8. body structural description
9. emotion-in-body
10. interoception
11. multisensory integration
12. peripersonal space
13. postural schema
14. somatoperception
15. superficial schema

ABSTRACT

The perception of our body is mediated by cortical representations of the body and the space around it. Body representations are constantly updated by the integration of interoceptive and exteroceptive signals during environment-body interactions. Research in the last years has distinguished multiple body representations, with specific functions, whose number and characteristics are still debated. This chapter provides a synthetic, critical overview of 1) the main taxonomies and 2) methods to study body representations; 3) key examples of plasticity in body representations, due to experimental manipulations, development, aging,

pathologies; 4) current knowledge about the neural correlates and 5) some crucial open issues.

1. What are body representations?

Our own body is at the same time a *medium* of perception and action: we perceive external stimuli through our body and we act in the world using our body parts. Importantly, our body is also itself an “object” of perception because we can perceive and have direct experience of it.

The body is represented at different levels in the central nervous system. Most studied body representations concern neural circuits underlying somatosensory and motor function. The primary somatosensory (S1) and motor (M1) cortices are somatotopically organized, with distinct brain areas receiving information from, and controlling the movements of specific body parts (Makin, Diedrichsen and Krakauer, 2020). However, body representations are not limited to tactile sensation or muscle activations, rather it involves multiple levels of processing of bodily information, that are crucial for controlling the body in the action-perception loop.

Body representations could be defined as patterns of neural coding occupying specific brain areas (or a network of brain areas, see paragraph 6) encoding and tracking the state of the body in time and space (De Vignemont, 2016; Riva, 2018). Indeed, in addition to tactile and motor cues, other modalities convey bodily information to the brain (e.g., the vision of the body, proprioception, vestibular processing, interoception) and no modality in isolation is sufficient to provide a full representation of the body for perception and action. Rather, a continuous, rich flow of multisensory information is processed bilaterally between the body and the brain, and contributes to body representations.

To give an example, we can focus on the representation of the size and shape of body parts. In order to efficiently perform a reaching movement, it is necessary to “know” the location of the different parts of the upper limb in space, thus combining information about posture, processed by proprioceptive afferent cues from receptors in joints, tendons, muscles and skin, with information about the dimensions of body segments (Longo and Haggard, 2010; Longo, 2018). However, no afferent signals directly convey information to the brain about the size and shape of body parts. Thus, authors have proposed that metric information about a body part likely arises from a central representation of the body part’s size and shape, an “offline body model” (Longo and Haggard, 2010) (see below), which is combined with online afferent and efferent inputs related to that body part.

Body representations are not limited to metric information about the body, but authors proposed multiple representations of the body in line with different models or taxonomies. Although no consensus has been reached so far on the exact number and functions of different body representations (Kammers *et al.*, 2010; Canzoneri, Ubaldi, *et al.*, 2013), in this

chapter we first summarize a (non-exhaustive) list of the most known taxonomies proposed so far (see Table 1).

Then, referring to, but also going beyond these taxonomies, we summarize the most common methods used to assess body representations. Body representations are not fixed, but they are shaped as a function of experience. Studying plasticity has provided important insight into the main features of body representations and their potential neural correlates. Thus, we present some paradigmatic studies describing plastic modifications of body representations after experimental manipulations, during development, aging and in pathologies and we will summarize current knowledge about the underlying neural correlates. Thus, finally, we highlight some of the most crucial open issues in the field.

2. Main theoretical models describing body representations

A description of body representation taxonomies is provided in Table 1.

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The original distinction between body for action and for perception is reflected in the *dyadic view* of body representations, distinguishing body schema and body image respectively (Head and Holmes, 1911; Gallagher, 2006; Dijkerman and de Haan, 2007; De Vignemont, 2010; Cardinali *et al.*, 2011). Following De Vignemont (2010), in addition to a functional distinction (action versus perception), this taxonomy is also based on two other main criteria, whose importance varies among different authors: availability to consciousness (unconscious, implicit versus conscious, explicit) and dynamics (short-term, on-line versus long-term, off-line).

Other authors have proposed a *triadic taxonomy of body representations*, where besides the concept of body schema, the notion of body image is further divided into a visuospatial representation indicated as a body structural description, a topological map of the body more related to perception, and a conceptual representation, i.e., body semantics (sometimes called simply “body image”) (Schwoebel and Coslett, 2005) interfacing with language (Sirigu *et al.*, 1991; Schwoebel and Coslett, 2005; Raimo *et al.*, 2019). This distinction among body representations has been based on dissociations in neuropsychological syndromes observed in post-stroke patients such as apraxia, viewed as disruption of the body schema, autotopagnosia, interpreted as an impairment in the body structural description, and body-specific aphasia, a disturbance of body semantics (Schwoebel and Coslett, 2005).

In addition, Longo and Haggard (2010) proposed a more complex model where body representations are further distinguished between *somatosensation*, i.e., higher level percepts of the body and objects contacting the body (“what the body is felt to be like”), and *somatorepresentation*, i.e., abstract knowledge, beliefs, and attitudes about bodies (“what the body is believed to be like”) (Tamè, Azañón and Longo, 2019)(see Table 1 in Longo *et al.*, 2010). Going beyond *somatosensation*, i.e., primary sensory processing of somatic stimuli,

somatoperception includes superficial schema and postural schema. The superficial and postural schemas were first postulated by Head and Holmes (1911) to account for the impairments of patients able to detect touches, without being able to localize those touches, i.e., a deficit in superficial schema, and patients with preserved ability to localize touches, but with impaired ability in localizing the spatial position of their stimulated limb, i.e., a deficit in postural schema. Somatosensation also consists of a representation of the metric characteristics of body parts, i.e., the body model (see above) and two other body representations capturing more conscious aspects such as body image and “emotion-in-body” (see Table 1).

Most recently, Riva (2018) has proposed a new theoretical model of body representations, including unique representations emerging during distinct developmental periods and based on both the online integration of incoming interoceptive and exteroceptive signals, as well as stored representations of the body, defined as “body memory”. In this view, the bodily experience is constructed during early development through the continuous integration of sensory and cultural data from six different representations of the body, also strictly related to the development of the self (see paragraph 1.7). The first three body representations (*Sentient Body*, *Spatial Body*, *Active Body*) are linked to the concept of body schema and include an egocentric point of view (the body as a reference of first-person experience). The latter three body representations (*Personal Body*, *Objectified Body*, *Social Body*) concern reflective knowledge about the body and are required to map the body using an allocentric view (the body as an object of third-person experience), thus referring more to the concept of body image (see Figure 2 in Riva, 2018). These six body representations (detailed in Table 1) are integrated in a coherent supramodal multisensory representation of the body and the space surrounding the body, called the “body matrix” (Moseley, Gallace and Spence, 2012; Dijkerman and Lenggenhager, 2018a).

Interestingly, unlike other taxonomies, Riva includes the representation of the space surrounding the body in his model. This is a particular sector of space, called *peripersonal space (PPS)*, where all interactions between the body and the environment take place. It has been originally studied by neurophysiologists conducting single-neuron recordings in non-human primates. They observed multisensory neurons in fronto-parietal areas of monkey responding to tactile stimuli on the body and also to external visual or acoustic stimuli, but only when presented within a limited distance from the body, defining the size of their multisensory receptive fields, which in turn defines the extent of PPS (Rizzolatti *et al.*, 1997; Avillac *et al.*, 2005; Graziano and Cooke, 2006; Cléry, Guipponi, Wardak, *et al.*, 2015; Serino, 2019). The existence of PPS representation and its multisensory propriety has been later confirmed by studies in humans. Works in neuropsychological patients with cross-modal extinction (e.g. di Pellegrino and Làdavas, 2015) or more recently in epileptic patients (Bernasconi *et al.*, 2018) and behavioural (Holmes, Calvert and Spence, 2004; Serino *et al.*, 2015) and neuroimaging studies (Bremmer *et al.*, 2001; Makin, Holmes and Ehrsson, 2008) in healthy participants, converges overall in demonstrating that PPS is coded by the special interaction between somatosensory signals from a specific body part (e.g., face, hand and

trunk, Serino et al., 2015) and external visual or acoustic stimuli presented close to that specific body part. Importantly, spatial constraints of multisensory interaction within PPS are defined in body-part centred reference frames, implying that proprioceptive and possibly vestibular information is also included in PPS representation. Thus, PPS representation is strictly related to the body, by integrating signals from different sensory systems, to interface information about the position of external stimuli and the body in space of potential body-environment interactions. PPS-related neural processes are also part of or directly project to the motor system (Rizzolatti *et al.*, 1997; Graziano and Cooke, 2006; Makin *et al.*, 2009; Serino, Annella and Avenanti, 2009) in order to transform multisensory representation of the body in space with respect to external stimuli into potentials re-actions. Thus, PPS representation has been proposed to mediate sensorimotor functions involved in approaching or defensive behaviours (Cléry and Ben Hamed, 2018), and also to constitute a primary interface between oneself and the external environment, implied in bodily self-consciousness (Serino, 2019).

In this chapter, in line with Riva's model, and previous authors already proposing a unique representation of the body in space as "a source or power for action" and interaction with the external world (Gallese and Sinigaglia, 2010), we include PPS in body representations. Supporting this choice, most authors have described at least two properties that body and space representations have in common. First, body and space representations are both built through the integration of multisensory signals (Maravita, Spence and Driver, 2003; Kandula *et al.*, 2017; Salomon *et al.*, 2017; Dijkerman and Lenggenhager, 2018). Additionally, body and space representations are not fixed, but plastically modified through the continuous flow of sensorimotor information arising from interactions with the environment (Maravita and Iriki, 2004; Martel *et al.*, 2016; Miller *et al.*, 2018). Before moving to presenting evidence underlying multisensory and plastic properties of body and space representations, we will describe the most known methods used to measure these representations.

3. Tasks to evaluate body representations

Any theoretical cognitive model is inherently linked to the possibility of measuring a given function. For body representations, there is a strict link between tasks used to measure body representations and their related taxonomies. As for the lack of consensus on body representation taxonomies, a conclusive and complete list of tasks assessing body and space representations is not possible. In Tables 2 and 3, we report some of the most commonly used procedures for identifying the crucial features of body representations.

<Table 2 near here>

In line with the dyadic view, tasks related to motor aspects or requiring a motor response, e.g., pointing to a body part (Paillard, 1999), action execution (Martel *et al.*, 2016), or motor imagery (see below), have been typically used to assess body schema. Taking this approach to its limits, some authors have also proposed that movement kinematics could be considered the ultimate measure of body schema (e.g., (Cardinali *et al.*, 2009b; Baccarini *et al.*, 2014;

Martel *et al.*, 2016). In contrast, other methods related to perceptual (e.g., (Kammers *et al.*, 2010), linguistic, e.g., naming of body parts (Paillard, 1999) or semantic aspects of the body (Sirigu *et al.*, 1991; Buxbaum and Coslett, 2001) have been proposed to study body image.

This subdivision between motor and perceptual aspects is also maintained in seminal work in stroke patients by Schwoebel and Coslett (2005) describing a battery of tasks aimed at proving dissociations among the body representations included in the “triadic view”. To assess body schema, tasks based on motor imagery and the “hand laterality task” were used (e.g., (Parsons, 1987). In contrast, tasks assessing body structural description required participants to localize body parts shown in pictures or by tactile inputs on the body. Such tasks aim to assess the spatial localization of body parts and localization of somatic sensations on the body surface, thus targeting postural and superficial schema respectively, in line with the models proposed by other authors (e.g., (Head, H., & Holmes, 1911; Longo, Azañón and Haggard, 2010). Finally, according to the triadic view, tasks targeting body image focus on instrumental aspects, i.e., “things that body part do”, clothing or tools.

However, these tasks (and taxonomies) did not include a metric representation of body parts, such as the perceived size and shape of the body parts, referred as the “*body model*” by Longo and Haggard (2010). This has received a growing interest in the last few years, by revealing important distortions in body perception. To capture a metric body representation, a task called body-landmarks localization task (BLT) has been proposed (see Table 2) (Longo and Haggard, 2010). In the BLT, the perceived location of anatomical landmarks on the participants’ upper limb is compared with their real position, so that actual and perceived dimensions are contrasted. This task is considered implicit because no explicit judgments about the width or length of the body parts are required (e.g., (Fuentes, Longo and Haggard, 2013; Longo, 2015a). Results obtained using the BLT consistently showed large and highly stereotyped distortions, i.e., an overall underestimation of finger length, with a gradient of increasing bias from the thumb to the little finger associated with overestimation of hand width (Longo, 2015a, 2018). Analogous results have been obtained by different labs (e.g., (Longo, Long and Haggard, 2012; Saulton *et al.*, 2016; Coelho, Zaninelli and Gonzalez, 2017) by adopting different versions of this task, assessing different postures of the hand (e.g., 90 degrees of rotation) (Longo and Haggard, 2010; Longo, 2015b; Saulton *et al.*, 2015) or using different modalities to give instructions about the target body parts (e.g., verbal or tactile instructions) (Cardinali *et al.*, 2011) or to report the perceived landmarks’ positions as verbal commands (Longo, Long and Haggard, 2012; Canzoneri, Ubaldi, *et al.*, 2013; Bassolino *et al.*, 2014; Longo, 2018) or movements (Peviani, Melloni and Bottini, 2019). Bias that consists in an overestimation of the width and underestimation of the length is also in line with results found using another implicit task based on tactile distance judgment, where participants are requested to judge the distance between two unseen tactile points on the hand. The tactile judgement along the hand’s width (medio-lateral direction) is overestimated compared to that along the hand’s length (proximo-distal direction) (i.e., anisotropies of perceived tactile distance) (Longo and Haggard, 2011; Longo, 2020). Authors underlined that this bias seems linked to the organization of the somatosensory system, as increased tactile acuity in the

transverse orientation on the limbs (Weber, 1834; Cody *et al.*, 2008; Longo and Haggard, 2011), and the characteristics of tactile receptive fields of both spinal (Brown, Fuchs, & Tapper, 1975) and cortical (Alloway, Rosenthal and Burton, 1989) neurons. These neurons are generally oval- (rather than circular) shaped with their long axis along the proximo-distal limb axis, so that two stimuli along the width of the hand are perceived farther apart because there is a larger number of unstimulated receptive fields between the stimulations (Longo, 2015a, 2020). Importantly, differences in receptive field size cannot account for the size of the bias, which is also affected by visual (Taylor-Clarke, Jacobsen and Haggard, 2004) or proprioceptive (De Vignemont, Ehrsson and Haggard, 2005) manipulations, implying that this judgement depends on cortical processing rather than pure sensory inputs. Another indirect measure of the perceived arm length is the “forearm bisection task” (Sposito *et al.*, 2012), where participants have to estimate the midpoint of their forearm, so that the position of the midpoint is taken as an index of perceived forearm length.

The metric characteristics of body representations have not only been evaluated using implicit tasks but also explicit tasks, where direct judgements on the perceived size of body parts are asked of participants in the “template matching task” (the most explicit one) and the “line length task” (Longo, 2015a). These tasks are similar to another procedure where participants are asked to adjust the length of a tape to match the perceived length of their arms (Linkenauger *et al.*, 2009). In line with Longo and colleagues’ view (Longo, 2015a), these tasks capture the conscious experience of our body (i.e., body image). In contrast to the consistent distortions found using the BLT, in the “template matching task”, participants on average select hands very similar to their actual hands (Gandevia and Phegan, 1999; Longo and Haggard, 2010), while in the “line length task”, distortions of perceived hand size and shape are qualitatively similar to those found in the BL, but are smaller in magnitude. Authors have interpreted these results by suggesting that, while the “template matching task” is mainly based on visual recognition processing, the “line length task” probably implies a larger contribution of somatosensory information related to one’s own body.

The “BLT” and the “template matching task” have been also adapted to evaluate metric characteristics of representations of the whole body (the Body Image Task, BIT) (Fuentes, Longo and Haggard, 2013) and of the lower limbs (Stone, Keizer and Dijkerman, 2018). Results from the whole-body equivalent reveal that participants overestimated the width of their shoulders and the length of their upper arms, relative to their height, while underestimating the lengths of their lower arms and legs. In contrast, when presented with a series of body templates with differing hip width/height ratios, participants selected the templates that most closely matched their true body dimensions, thus this mimics the results observed for the hand, with reduced distortions in the “template matching task” than in the “BLT”. Differently, distortions in lower limb representations occurred with both tasks (Stone, Keizer and Dijkerman, 2018; Peviani, Melloni and Bottini, 2019).

Another class of tasks focus on the assessment of the configuration/location, rather than the dimension, of the different body parts. They are derived or inspired by the test proposed by Daurat-Hmeljiak *et al.* (Daurat-Hmeljiak, C., Stambak, M., Berges, 1978) and adapted as the

Frontal Body Evocation task (FBE) (Di Vita *et al.*, 2019; Raimo *et al.*, 2019), whereby participants are asked to place different body parts on a template space, and the relative positions are used to estimate whole body perception. This approach asks the subject to refer one's own body perception to a "standard model" (e.g., template, avatar, figures). A recent implementation of this approach has used virtual reality or computer graphics to present participants with a modifiable body model and asks them to make as "you perceive", "think", "feel", "would like" your body to be (see (Riva, Melis and Bolzoni, 1996; Letosa-Porta, Ferrer-Garcia and Gutiérrez-Maldonado, 2005). A complementary, low-tech, approach consists in the use of self-portraits, where participants are asked to realize a drawing of their whole body. This, for instance, has been used in post-stroke patients (Bach, Tracy and Huston, 1971; Morin *et al.*, 2003) and children with cerebral palsy (Lampe *et al.*, 2016; Nuara *et al.*, 2019). The comparison between the reproduction of an affected vs. non-affected body part is used to evaluate alterations in body representations due to sensorimotor or cognitive deficits (e.g., asymmetry in the arm length of hemiplegic patients; a lack of a mouth in patients with speech disorders).

Concerning the representation of space around the body, many behavioral tasks have been proposed to measure PPS. Since previous reviews already detail these procedures (Cléry and Ben Hamed, 2018; Serino, 2019), we provide a concise list detailed in Table 3.

<Table 3 near here>

Two main tasks have been used to demonstrate the multisensory proprieties of PPS in humans, i.e., that the processing of tactile information on the body is more effectively influenced by visual or auditory stimuli occurring near to compared to far from the body: the crossmodal congruency task (e.g., (Spence *et al.*, 2004; Macaluso and Maravita, 2010; Occelli, Spence and Zampini, 2012) and multisensory reaction tasks (see (Serino *et al.*, 2015). Different versions of this latter task have been used by stimulating various body parts, such as the hand (Serino *et al.*, 2007, 2015; Bassolino *et al.*, 2010; Serino, Canzoneri and Avenanti, 2011), the face (Teneggi *et al.*, 2013), the trunk (Noel *et al.*, 2014, 2015) and the lower limbs (Stone *et al.*, 2020), and by using both static (Serino *et al.*, 2007; Bassolino *et al.*, 2010) and moving visual or auditory stimuli (Canzoneri, Magosso and Serino, 2012), neutral or emotionally relevant stimuli (Taffou and Viaud-Delmon, 2014; Ferri, Tajadura-Jiménez, *et al.*, 2015; de Haan *et al.*, 2016). This approach has been used in combination with other techniques, such as Transcranial magnetic stimulation (Makin *et al.*, 2009; Serino, Annella and Avenanti, 2009; Finisguerra *et al.*, 2015), scalp (Noel, Serino and Wallace, 2018) and intracranial (Bernasconi *et al.*, 2018) electroencephalography, and fMRI (e.g.(Makin, Holmes and Zohary, 2007; Brozzoli, Gentile and Ehrsson, 2012; Ferri, Costantini, *et al.*, 2015).

More recently, another implicit measure, based on a physiological response such as the *hand-blink reflex (HBR)* and its modulation as a function of the distance between the arm and the face, has been proposed to assess the representation of the so-called defensive PPS (de Vignemont and Iannetti, 2015; Bufacchi and Iannetti, 2018). This task evaluates the modulation of PPS as a function of sensorimotor processes, e.g., motor intention and

planning (Bisio *et al.*, 2017; Fossataro *et al.*, 2018); learnt posture (Biggio *et al.*, 2019), vestibular signals related to external gravity (Bufacchi and Iannetti, 2016), as well as higher-level aspects, such as personality traits (Sambo and Iannetti, 2013).

Finally, other measures have been proposed to capture a basic form of near-far differentiation in spatial processing, such as the *line bisection task* (Longo and Lourenco, 2006, 2007) and *reachability judgements* (Costantini *et al.*, 2010; Cardellicchio, Sinigaglia and Costantini, 2011; Delevoye-Turrell, Vienne and Coello, 2011). However, these tasks based on reachability judgments capture a larger, shoulder-centered representation of the reaching space that is distinguished from a multisensory body-parts-centered PPS representation sustaining both proactive and defensive behaviors (De Vignemont *et al.*, in press; Zanini *et al.*, 2020).

4. Plasticity of body representations: experimental manipulations, changes during the lifespan and pathologies

Experimental manipulations. One of the most interesting characteristics of body representations is their plasticity. Indeed, body representations are constantly updated by the continuous bi-directional flow of multisensory information between the body and the brain. In adults, under natural circumstances, such a flow of information is usually stable within a range of normal variability. Conditions, however, might vary due to several factors, such as specific sensorimotor training, damage to the body or the brain, or during the lifespan (e.g., development or aging). A large body of empirical evidence – summarized in this paragraph – has demonstrated that body representations reshape accordingly, as a function of these changes.

A classic example of the plasticity of body representations is linked to changes in the flow of information between the body and the brain, as in the case of experimentally-induced anesthesia. Cutting off inputs from the peripheral nerves with cutaneous anesthesia produces an increase in the explicit perceived dimension of the anaesthetized body-parts (e.g., the hand, (Gandevia and Phegan, 1999) or the mouth, (Türker, Yeo and Gandevia, 2005) and see (Giurgola *et al.*, 2019) for TMS-induced changes of the explicit perceived dimension of the hand).

On the other hand, multisensory stimulation has also been shown to affect body representations (see also (Taylor-Clarke, Jacobsen and Haggard, 2004; Bruno and Bertamini, 2010; Tajadura-Jiménez *et al.*, 2012). For instance, the perception of body form can be altered using the so-called Pinocchio illusion (Lackner, 1988). Here, an illusory elongation of the nose is reported when a vibration inducing sensation on the arm extension is applied on the arm touching the nose. De Vignemont, Ehrsson, and Haggard (2005) used a bimanual version of the Pinocchio illusion to create an illusory elongation of one finger, and found that during the illusion, stimuli on that finger were perceived as farther apart as compared to a no illusion condition (De Vignemont, Ehrsson and Haggard, 2005).

In addition, body representations can be affected by changes in limb use, such as disuse or overuse. In an experiment conducted on healthy volunteers, Bassolino et al. (Bassolino *et al.*, 2014) observed that 10 hours of upper limb immobilization reduces PPS representation around the immobilized arm (see also (Toussaint *et al.*, 2018) for a similar effect on reaching judgements). Unlike tool-use (see below), perceived arm length was not modified by disuse, but by increased use of the free non-dominant limb during the immobilization of the dominant one. The overuse of the free limb did not affect the PPS representation, thus suggesting a dissociation in the plasticity of PPS and body representations.

Moreover, many studies have demonstrated that body representations are also affected by the way the body acts in space, such as when using tools (e.g., rake or pliers) to reach out of reach objects, i.e., in far space (Maravita and Iriki, 2004; Martel *et al.*, 2016; Cléry and Ben Hamed, 2018). Studies have demonstrated that tool-use re-shapes body representations by extending the estimated length of the tool-holding limb or by altering the limb kinematics after tool-use (Cardinali *et al.*, 2009a; Sposito *et al.*, 2012; Canzoneri, Ubaldi, *et al.*, 2013). Other studies have shown modifications of PPS representations after tool-use. In non-human primates, while PPS neurons are normally coding tactile stimuli on the hand, visual stimuli presented close to the hand also start responding to visual stimuli located further in space, where the tool was used (Iriki, Tanaka and Iwamura, 1996; Maravita and Iriki, 2004). Similarly, studies with both healthy participants and patients have found that, after tool-use, multisensory interactions between tactile stimuli on the body and visual or auditory cues presented close to the body are also extended to stimuli located in far space, in particular at the location where the tool was used (Farnè and Làdavas, 2000; Maravita *et al.*, 2001; Holmes, Calvert and Spence, 2004; Galli *et al.*, 2015). Plasticity effects for active tool-use was reported after short experimental training (typically around 15/20 minutes, (Canzoneri, Ubaldi, *et al.*, 2013; Garbarini *et al.*, 2015) or long-term, everyday life use of specific tools in different populations, such as blind people using a cane (Serino *et al.*, 2007), computer mouse users (Bassolino *et al.*, 2010) or professional tennis players (Biggio *et al.*, 2017).

Changes during the lifespan. As well as experimental manipulations, normal life can affect body representations. This is surely the case during childhood or adolescence when the structure of the body grows with an extraordinary velocity.

Some authors have suggested that a multisensory PPS representation (e.g., (Orioli *et al.*, 2019) and a “rudimental” body schema (e.g. Rochat, 2010) exist at birth and possibly even before, in the prenatal period. In line with this, recently an electrophysiological pattern of multisensory integration modulated by the proximity to the body has been shown in 16-92 hours old newborns, suggesting a primitive coding of the bodily-self boundaries, already within the first hours of life (Ronga *et al.*, in press).

In contrast, it has been proposed that body image develops over the course of childhood (Slaughter and Brownell, 2011).

The ability to integrate proprioceptive/postural and tactile bodily cues seems to also develop quite early (e.g. Crucianelli and Filippetti, 2020), as shown by the influence of body posture

on tactile discrimination observed in babies as young as 8 months (Begum Ali, Spence and Bremner, 2015). Many studies in older children then focused on the development of specific body representations (see Table 1 in (Raimo *et al.*, 2019)). For instance, Raimo and colleagues (2019), in line with the triadic view, assessed three body representations in the same sample of children and found body semantics (tested with the Object-Body Part Association task) was completely developed in school-aged children, body structural representation (assessed with the Frontal Body-Evocation subtest) reached an adult-like pattern by the age of 9–10 years, while this was not the case for body schema, evaluated with a hand laterality task. Although during infancy, the body height and weight changes enormously, few studies have focused on metric representation in children. Recently a study investigated a metric body representation of the hand in children aged between 6 and 10 years old and showed a bias, i.e., underestimation of the whole hand size, evaluated via haptic or visual information, that increases with development (Cardinali, Serino and Gori, 2019) The idea of a distorted hand metric representation in young children is in line with another recent studies showing finger length underestimation increasing with age in children and adolescents (Van der Looven *et al.*, 2021)

Another period of life in which the body rapidly changes is during pregnancy. Empirical findings show an enlargement of PPS representation, with a shallower gradient between peripersonal and extrapersonal space in the third trimester, but not in the early weeks of pregnancy or post-partum (Cardini *et al.*, 2019). In addition, a study based on a self-report questionnaire on how women experience their body during pregnancy demonstrated that women who felt more positively about their body changes were better at interpreting their interoceptive signals (Kirk and Preston, 2019).

Finally, it has been recently hypothesized that body representations could be affected in healthy older people because of the functional decline in primary sensory inputs and/or motor function (Costello and Bloesch, 2017; Kuehn *et al.*, 2018), altering the bidirectional flow of information from the body to the brain and vice-versa. In line with this hypothesis, it has been recently found that older participants underestimated the perceived length of their arm with respect to younger participants (Garbarini *et al.*, 2015; Sorrentino *et al.*, 2021), while their multisensory PPS representation seem to be more similar (Sorrentino *et al.*, 2021). Interestingly, also the plasticity of body representations and spatial representation are likely altered in aging. For instance, reduced plasticity of spatial representations related to the reaching space has been observed in older adults after tool-use (Caçola, Martinez and Ray, 2013; Costello *et al.*, 2015). Similarly, older participants seem impaired in integrating rapid changes in body state during motor imagery, e.g., when a load is worn on their arm (Personnier *et al.*, 2008).

Pathologies. Following brain lesions, in particular due to stroke, several symptoms involving the representation, but also the experience of the body (e.g., the experience of having a body, i.e., body ownership, and of being in control of it, i.e., a sense of agency) have been described and reviewed elsewhere (see Table 4) (Haggard and Wolpert, 2005; de Vignemont, 2010a; Riva, 2018; Ronchi, Park and Blanke, 2018; Case *et al.*, 2019).

<Table 4 near here>

The majority of these symptoms have been studied in stroke patients (e.g., asomatognosia, (Romano and Maravita, 2019); somatoparaphrenia, (Vallar and Ronchi, 2009); personal neglect, e.g. (Caggiano and Jehkonen, 2018); pathological embodiment, (Garbarini *et al.*, 2015; Pia *et al.*, 2020); alien hand syndrome, (Hassan and Josephs, 2016); auto/heterotopagnosia, (Wicky, 2005; Bassolino *et al.*, 2019), for reviews see (van Stralen, van Zandvoort and Dijkerman, 2011; Rousseaux, Honoré and Saj, 2014; Oouchida *et al.*, 2016). Evidence following the classic neuropsychological approach based on double dissociations has been also been used to support the existence of difference body representations. Typically, the description of a patient showing a deficit on one specific body representation task (following a particular brain lesion) with relatively preserved performance on another body representation task, and the report of another patient demonstrating the opposite pattern of performance (following a different lesion) has been taken as proof for the existence of two distinct body representations. This is the approach of the large study by Schwoebel and Coslett (2005), where the dissociations found in the performance of 70 stroke patients on tasks proposed to assess body schema, body structural description and body semantics supported the distinctions among these body representations (see also (Rasmus, 2017; Di Vita *et al.*, 2019b).

On the other hand, disorders in body representations can arise after brain lesions, not only because of direct damage to the key areas underlying body representations (see next paragraph), but also because of the reduced bidirectional flow of sensorimotor information from/to the body and the brain (e.g., (Oouchida *et al.*, 2016), i.e., in the case of hemiplegia and/or somato-hemianesthesia. Recently, body representation tasks have been used to study the co-occurrence of body representations and motor and/or somatosensory deficits in stroke patients. Significant distortions in the metric representation of the contralesional arm, characterized by underestimation of the arm length, have been reported in stroke patients (Bassolino *et al.*, submitted; (Tosi, Romano and Maravita, 2018). Similarly, alterations in the metric representation of the limb (i.e., an asymmetry in the perceived length of the affected arm revealed through self-portraits) have been also reported in children affected by cerebral palsy (Nuara *et al.*, 2019).

Moreover, considering the plasticity properties of body representations, one could hypothesize that any pathological condition affecting the flow of information between the body and the brain or altering the physical structure of the body could lead to alterations in body representations. Although not complete, here we describe some of the most known and inspiring examples.

Body representation changes have been observed after dramatic alterations in the flow of information between the body and the brain because of peripheral damage such as deafferentation and spinal cord injuries (SCI). Cardinali *et al.* (Cardinali *et al.*, 2016), for instance, showed altered plasticity of body representations following tool-use in a deafferented patient, suggesting a key role of proprioception in shaping body

representations. Altered body representations have been reported following SCI. These patients typically perceive their deafferented torso and limbs as elongated relative to their body width (Fuentes *et al.*, 2013). Moreover, various corporeal illusions involving body form (sensations of body loss and body-part misperceptions), body motion (illusory motion), and body ownership (disownership-like feelings and somatoparaphrenia-like feelings) have been reported in patients with SCI and were related to neuropathic pain (Scandola *et al.*, 2017). Higher prevalence of depersonalization symptoms (Lenggenhager *et al.*, 2012), with increased detachment from their internal bodily sensations and decreasing global body ownership, and a reduced sensitivity to multisensory stimulation inducing illusory leg ownership (Pozeg, Galli and Blanke, 2015) have been also described in SCI. Finally, PPS representation seems altered in patients with SCI, with a reduction of PPS size around the body parts below (e.g., around the feet), but not above (e.g., the hand), the lesion level (Scandola *et al.*, 2016).

In addition, body representation modifications have been reported after alterations in the physical structure of the body, such as limb amputation (Canzoneri, Marzolla, *et al.*, 2013; Rognini *et al.*, 2018). In amputees, there are not only alterations in primary sensorimotor representations (e.g., see Makin, Diedrichsen and Krakauer, 2021; Buonomano and Merzenich, 1998; Serino and Haggard, 2010), but also modifications of body representations such as, (i) an underestimation of the phantom limb or stump's perceived length ("telescoping", e.g., (Ramachandran and Rogers-Ramachandran, 2000; Canzoneri, Marzolla, *et al.*, 2013; Rognini *et al.*, 2018), (ii) alterations in phantom limb shape or weight (thus it is perceived as swollen, stuck in a position and heavy, see (Giummarra *et al.*, 2010)), (iii) a shift of PPS boundaries towards the stump (Canzoneri, Marzolla, *et al.*, 2013), (iv) impaired ability to represent relations among different body parts (Palermo *et al.*, 2014), (v) or an enhanced difficulty in performing a motor imagery-based hand laterality task (Nico *et al.*, 2004). Conversely, wearing functional prosthesis ameliorates the perceived length of the phantom (Canzoneri, Marzolla, *et al.*, 2013; Rognini *et al.*, 2018), while it seems that aesthetic prosthesis does not improve motor imagery (Nico *et al.*, 2004). Interestingly, the same distortion in the representation of the hand found in healthy participants – namely, the hand is perceived as shorter and wider than it really is (see above) – has also been described in an amputee concerning her phantom limb (Longo, Long and Haggard, 2012). Finally, another case of alteration in body structure reflecting body representation distortions is the case of achondroplastic dwarfs where altered topological maps of the body are improved after surgical extension of the lower limbs (Di Russo *et al.*, 2006; Cimmino *et al.*, 2013).

Case and colleagues (Case *et al.*, 2019) recently summarized body representation alterations also in psychiatric disorders, such as anorexia nervosa or schizophrenia. In individuals with anorexia nervosa, distorted bodily perceptions have been described in the visual (e.g., visual body size, (Cash and Deagle, 1997)), tactile (e.g., (Keizer *et al.*, 2011, 2012), motor (e.g., (Guardia *et al.*, 2010)) and multisensory (Gaudio, Brooks and Riva, 2014) domains or at the level of interoceptive awareness (e.g., (Fassino *et al.*, 2004)). This evidence has been used to suggest that dissatisfaction with body size in this pathology might not be purely cognitive-

affective, but also depends on bodily perceptual distortions. Patients with schizophrenia are known to experience problems with self-perception, such as self-recognition and self-attribution of thoughts and actions (Schneider, 1950), but also in body perceptions, as in body structural descriptions (e.g., (Graham-Schmidt *et al.*, 2016), self-other distinctions (Farrer *et al.*, 2004), multisensory bodily perceptions (Cascio *et al.*, 2019) and PPS (Di Cosmo *et al.*, 2018).

Finally, patients suffering from chronic pain often show abnormalities in their body representations. For instance, patients with complex regional pain syndrome (CRPS) are often impaired in recognizing their own limb (Moseley, 2004) and estimating its position (Lewis *et al.*, 2010), its size (by perceiving their affected limb to be larger than how it really is (Moseley, 2005) and its orientation (Schwoebel, 2001; Legrain *et al.*, 2012). Moreover, patients with CRPS typically report feelings of foreignness (Förderreuther, Sailer and Straube, 2004), strangeness, alterations in ownership/agency or even hostility toward the painful limb (Galer and Jensen, 1999; Case *et al.*, 2019) and seem to neglect the side of space where the affected limb normally resides (Legrain *et al.*, 2012). In patients with trigeminal neuralgia, stimuli applied to the ipsilateral hand elicited a strong hand-blink reflex, if it was measured from the ipsilateral eye, a result interpreted as an expansion of defensive PPS around the painful side (Bufacchi *et al.*, 2017). Recently in a systematic review, Viceconti and colleagues (Viceconti *et al.*, 2020) summarized body distortions emerged in implicit and explicit tasks targeting somatoperception in patients with chronic pain because of musculoskeletal disorders and rheumatic diseases.

Overall, alterations in body representations have been reported so far in patients with central (e.g., stroke, cerebral palsy) or peripheral (e.g., SCI) disorders, structural (e.g., amputation, dwarfs) or psychiatric (anorexia nervosa, schizophrenia) diseases or with chronic pain (neuropathic or linked to musculoskeletal or rheumatic pathologies).

5. Neural networks underlying body representations

In this final section, we summarize the most up-to-date evidence of the neural underpinnings of body representation, as conceptualized by the taxonomies described above (see Table 5). A classic neuropsychological approach has been followed by some authors to localize the different body representations into specific brain areas, as a function of the localization of brain lesions of patients demonstrating rather selective body representation impairments.

<Table 5 near here>

In line with the dyadic view, a first subdivision was proposed between dorsal fronto-parietal lesions, mainly associated with deficits in body representations for action, i.e., body schema, and ventral parieto-temporal lesions, mainly associated with body representations for perception, i.e., body image (De Vignemont, 2010), reminiscent of the dorsal/ventral, “what”/“where” distinction proposed for visual (Milner and Goodale, 1992) or

somatosensory (Dijkerman and de Haan, 2007) processing. Evidence for such a distinction comes from double dissociations in neurological patients, such as the one described by Paillard (G Berlucchi and Aglioti, 1997; Paillard, 1999; Berlucchi and Aglioti, 2010). He described the deficit of a “centrally deafferented” patient after a parietal stroke who, although unable to consciously detect the presence of a tactile stimulus, was able to point to the precise position which had been stimulated by the examiner (“blind touch”), as an alteration of the body image with preserved body schema. In contrast, the behaviour of another patient, “peripherally deafferented” after neuropathy, who was able to identify body parts touched out of sight, but was not able to point to them without vision (i.e., sensory detection without localization), was attributed to a body schema deficit, in the presence of a spared body image.

Consistent with this approach, but following the triadic view, Schwoebel and Coslett (Schwoebel and Coslett, 2005) reported more common involvement of fronto-parietal areas in stroke patients showing deficits on body schema tasks and of temporal regions in stroke patients with deficits in body structural description and body semantics tasks.

Longo and Haggard reviewed evidence from multiple studies in order to describe the neural correlates of the distinct body representations that are part of somatoperception, as summarized in Table 5 (Longo, Azañón and Haggard, 2010). Recently, it has been shown that the reconstructed shape of the hand in the primary somatosensory and motor cortices matches the distortions that emerge at behavioural level, thus suggesting the involvement of sensory-motor cortices in the metric representation of the hand (Tamè *et al.*, 2021)..

Besides focusing on a list of associations between more or less specific brain areas and more or less selective symptoms, and considering that perceiving the body requires processing and integration of multiple bodily signals, we believe that a more powerful approach is to study the neural correlates of body representations in terms of information flow and integration of the different bodily cues contributing to them. In line with this view, a network of unisensory and multisensory areas interacting with one another sub-serves body representations (Serino *et al.*, 2013) (Figure 1).

<Figure 1 near here>

Accordingly, multiple unisensory areas contribute to body representations, namely regions underlying:

- (i) motor processing - the primary motor cortex, M1, and higher order motor regions, such as the supplementary motor area and premotor cortex (Melzack, 1990; Berlucchi and Aglioti, 1997; Berlucchi and Aglioti, 2010; Daprati, Sirigu and Nico, 2010; Naito, Morita and Amemiya, 2016),
- (ii) sensory, tactile and proprioceptive, functions – the primary somatosensory cortex, SI, posterior parietal cortex, PPc, intraparietal sulcus, IPS (for reviews see (Longo, Azañón and Haggard, 2010; Serino *et al.*, 2013),
- (iii) visual bodily inputs - the extrastriate body area, EBA, e.g., (Grossman and Blake, 2013),

- (iv) vestibular signals - the temporo-parietal junction, TPJ (Tsakiris, 2010a; Blanke, 2012), and
- (v) interoceptive and affective information - the insula (Dijkerman and de Haan, 2007; van Stralen *et al.*, 2018).

These unisensory signals are integrated in multisensory regions in the posterior parietal cortex (PPc; e.g., (van Stralen, van Zandvoort and Dijkerman, 2011), and specifically the superior parietal lobule (SPL, e.g., (Corradi Dell'Acqua, Tomasino and Fink, 2009; Saetta *et al.*, 2020)), the inferior parietal lobule (IPL, e.g.(van Stralen, van Zandvoort and Dijkerman, 2011; Di Vita *et al.*, 2019b), and the intraparietal sulcus (IPS, e.g.(Corradi Dell'Acqua, Tomasino and Fink, 2009), as well as the ventral premotor cortex (vPMc), the TPJ, the insula and the secondary somatosensory cortex (for a review see (Tsakiris, 2010b; Serino *et al.*, 2013). The power of this approach in better describing the complex brain network underlying body representations has also been demonstrated in explaining bodily deficits. For instance, a recent study in stroke patients (Di Vita *et al.*, 2019) has shown that a deficit in body structural description (assessed using the frontal body-evocation subtest) is better explained by disconnection within a network encompassing regions in the temporal (i.e., middle and superior temporal gyrus extending to the TPJ), parietal (i.e., postcentral gyrus; angular gyrus, and supra-marginal gyrus), frontal (i.e., middle and inferior frontal gyri as well as precentral gyrus) and insular cortices (anterior insula and putamen), rather than by localized lesions.

A network approach has also describes the neural correlates of PPS. A recent meta-analysis (Grivaz, Blanke and Serino, 2017), aimed at identifying consistent activation from neuroimaging studies, directly compared activation associated with processing near vs. far space. This paper identified a network of regions including unisensory and multisensory areas, located bilaterally in the superior parietal cortex, the temporo-parietal cortex and the premotor cortex, plus the putamen. Further analysis of the same work by Grivaz and colleagues revealed functional connections involving the IPL and IPS regions with primary somatosensory regions, and between the SPL and premotor regions (see Figure 1). This network largely corresponds to the regions where the populations of PPS neurons have been described in non-human primates (Fogassi *et al.*, 1996; Rizzolatti *et al.*, 1997; Graziano and Cooke, 2006). This suggests that in humans, as in monkeys, PPS representation is supported by interconnected frontal and parietal regions, constituting one of the several fronto-parietal networks (Makin, Holmes and Ehrsson, 2008) involved in sensory-motor processes mediating individual-environment interactions (Serino, 2019).

6. Open issues and conclusions

The question of how we perceive our own body and the space around it has received growing attention in the last years. Many studies, reviews (e.g., De Vignemont, 2010; Gallese and Sinigaglia, 2010; Cléry, Guipponi, Odouard, *et al.*, 2015; Longo, 2015a; Bufacchi and Iannetti, 2018; Cléry and Ben Hamed, 2018; Serino, 2019; Viceconti *et al.*, 2020), chapters (e.g., (Ronchi, Park and Blanke, 2018; Case *et al.*, 2019), special issues (e.g., Tessari *et al.*, 2010;

Dijkerman and Lenggenhager, 2018) and conferences (e.g., the BRnet conference <https://bodyrepresentation.wixsite.com/brnet>) have been specifically dedicated to this topic, and the main conclusions from this research effort have been summarized in the previous paragraphs. However, several issues remain still open.

First, there is no consensus on the definitions of body representations. Although the majority of authors agree in proposing some macro-categorization, such as a distinction between implicit and explicit representations (Longo, 2015a)(see Table 1), how a distinct body representation, among the multiple representations proposed, belongs to one or another category is a matter of debate. Here, we propose a general representation of the various dimensions according to which body representations have been presented, with the aim of helping the reader to orient (see (Bufacchi and Iannetti, 2018; Noel and Serino, 2019; Serino, 2019)). This view suggests that, rather than computing a number of distinct representations, different properties or characteristics of a body model stored in the brain are accessed when certain sensory modalities are processed, and functional responses are required.

Moreover, although these representations arise from the integration of unisensory and multisensory processes, the weight of each modality in body representations is unclear. This has not only a theoretical value for the conceptualization of body representations, but it could also better explain body distortions and deficits, whereby some pathological alterations in the perception of one's own body can be explained by deficits in unisensory functions or in their multisensory integration. This would eventually help in designing interventions, based on the mechanisms underlying body representations, to treat patients or improve healthy development and aging.

Among the multiple sensory modalities contributing to body representations, in this chapter we focus on exteroceptive cues. However, an important component of bodily processing relies on interoception, i.e., the processing of internal bodily signals (e.g., breathing or heartbeat) from visceral organs. This topic, which has critical relevance for subjective experience and behavior, is receiving increasing attention in the field, as underlined in dedicated reviews (see (Craig, 2002; Seth and Tsakiris, 2018; Park and Blanke, 2019)). Future work will clarify how exteroceptive and interoceptive cues are integrated into body representations.

Finally, multisensory information, including interoceptive signals that build and update body representations, as well as the relative underlying neural correlates of these inputs, are also involved in the conscious experience of the self within the boundaries of the physical body, i.e., bodily self-consciousness (BSC, e.g., (Blanke, Slater and Serino, 2015)). The body is indeed strictly related to the self, since we feel ownership of our body parts (i.e., the hand that is writing is my own hand) and agency for the actions we perform (i.e., I am the one who is writing), we locate ourselves where we perceive our body to be through proprioceptive and vestibular inputs (self-location) and we perceive the world from our body's location (first-person perspective). In line with this view, Blanke and colleagues (Blanke, Slater and Serino, 2015) indicate 4 main constraints of BSC in which the body has a key role. More specifically, BSC (i) depends on proprioceptive and vestibular inputs signaling the location of body parts and of the whole body in space (proprioceptive constraints); and on (ii) visual information

about the shape and the structure of the body (body-related visual information constraints), (iii) it is linked to PPS, (iv) it can be altered by prolonged multisensory stimulations that reshape the PPS boundaries and induce BSC for non-corporeal objects (embodiment constraints).

In conclusion, given the complexity and the richness of the current research in the field, without pretending to be exhaustive and definitive, in this chapter we have provided a summary of the core concepts in body representation research, with a particular attention on the multisensory nature and the plasticity features of body representations. This is still an open field of study in neuroscience and psychology, with important applications for other disciplines, such as medicine, education, and robotics.

Figure legends

Figure 1. On the left, a schematic representation of the network of unisensory and multisensory areas mainly involved in body representations (adapted from Serino et al., 2013), while on the right, the results of the meta-analysis on PPS representation conducted by Grivaz et al. 2017 (from Grivaz et al., 2017). Only one hemisphere is showed for schematic purposes. (M1: primary motor cortex, S1/S2: primary/secondary somatosensory cortex, SPL: superior parietal lobule, IPL: inferior parietal lobule, IPS: intraparietal sulcus, PMv/d: ventral/dorsal premotor cortex, TPJ: temporo-parietal junction, EBA: extrastriate body area).

Acknowledgements. We thank Silvia Serino and Giulio Mastria for suggestions on the manuscript, Petr Grivaz and Michel Akselrod for their help with Figure 1.

Funding. This work was supported by a SNSF Professorship Grant MYSPACE (PP00P3_163951/1) to AS and by the “Fondation Pierre Mercier pour la Science” grant to MB.

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Table 1

DYADIC VIEW	TRIADIC VIEW	SOMATOPERCEPTION	BODY MEMORY
<p>1. BODY SCHEMA: an implicit, online adapted sensorimotor representation of body parts' size and position for action, based on afferent and efferent information</p> <p>2. BODY IMAGE: a more explicit, offline updated, representation of body appearance for perception and for conceptual or emotional aspects</p>	<p>1. BODY SCHEMA: see diadic view</p> <p>2. BODY STRUCTURAL DESCRIPTION: a topographical representation of the body primarily based on vision, but also on somatic perception, concerning the relationships between body parts, as their boundaries and their position relative to each other</p> <p>3. BODY SEMANTICS: a lexical-semantic representation of the body including body part names, functions, and association with objects</p>	<p>1. SUPERFICIAL SCHEMA a mapping of somatic stimuli on the body</p> <p>2. POSTURAL SCHEMA a representation of current body posture (i.e., joint angles), incorporating both afferent proprioceptive signals and efferent copies of motor commands</p> <p>3. BODY MODEL a representation of the metric properties (i.e., size and shape) of the body, capturing distortions that seem to mimic those of primary somatosensation</p> <p>4. CONSCIOUS BODY IMAGE an approximately veridical conscious perception of body form</p> <p>5. EMOTION-IN-BODY affective processing of and responses to somatic stimuli</p>	<p>1. THE SENTIENT BODY an invariant spatial structure integrating interoceptive signal with proprioceptive and vestibular sensitivities, present since birth</p> <p>2. THE SPATIAL BODY developed during the first 6 months of life, based on the integration of afferent sensory information in an egocentric frame</p> <p>3. THE ACTIVE BODY from 7 months, where afferent information are integrated with efferent information relating to the movement of the body in space</p> <p>4. THE PERSONAL BODY from 24 months, where the various components of BR are integrated in a coherent whole body-representation</p> <p>5. THE OBJECTIFIED BODY from 24/36 months, including a third-person representation of subject's own public body</p> <p>6. THE SOCIAL BODY from 48 months, where the objectified body is integrated in an allocentric view with social rules and narratives related to the body</p>

Table 1. A summary of the definitions of multiple body representations defined by the main theoretical models (taxonomies, first row), adapted from (diadic view: De Vignemont, 2010; triadic view: Raimo *et al.*, 2019, Schwoebel and Coslett, 2005; somatoperception: Longo, Azañón and Haggard, 2010; body memory: Riva, 2018).

Table 2

BR tasks in the DYADIC VIEW ^a	BR tasks in the TRIADIC VIEW ^b	BR tasks for SOMATOPERCEPTION ^d
<p>1. BODY SCHEMA: * e.g. pointing to a body part, kinematics, motor imagery</p> <p>2. BODY IMAGE: ^ e.g. naming or define functionally body parts</p>	<p>1. BODY SCHEMA: • <u>motor imagery</u>: * imagine making a specified movement, the duration of imaged and executed movement are compared • <u>hand laterality task</u>: * participants are shown a picture of a hand palm-up or palm-down condition and different orientations and are asked to indicate if the stimulus is the right or left hand</p> <p>2. BODY STRUCTURAL DESCRIPTION: • <u>localization of isolated body parts</u>: ^ point on their own bodies to parts that matched pictured body parts • <u>localization of tactile inputs</u>: ^ point to parts of a mannequin that corresponded to the location on their own bodies where a tactile stimulus was presented • <u>matching body parts by location</u>: ^ point to pictured body parts that is closest on the body surface to a target body part • <u>Daurat-Hmeljiak test /Frontal Body Evocation task</u>^c ^ participants are showed the picture of a child and then they were required to relocate a specific body part on a paper (or a screen in the Frontal Body Evocation task) where only the head is shown as reference</p> <p>3. BODY SEMANTICS:</p>	<p>1. SUPERFICIAL SCHEMA * e.g. localization of isolated body parts</p> <p>2. POSTURAL SCHEMA * e.g. localization of tactile inputs</p> <p>3. BODY MODEL • <u>body-landmark localization task (BL)</u> * participants are asked to judge the location of some anatomical landmarks, as the knuckles and tips of their fingers, that have been previously covered with an occluding board. To answer, participants place the tip of a long baton on the board, directly above each location or give <i>verbal commands</i> to an experimenter on how to move the baton or perform <i>movements</i> to match the perceived hand position with a visual target • <u>tactile distance judgement</u> * participants are asked to judge the distance between two unseen tactile points on the hand: estimates made along the hand's width (medio-lateral direction) are overestimated compared to estimates made along the hand's length (proximo-distal direction) • <u>forearm bisection task</u>^e * participants have to estimate the midpoint of one's own forearm, typically before and after an experimental manipulation (e.g. tool-use). The position of the midpoint is taken as an index of perceived forearm length, with a more distal (i.e. towards the hand) midpoint indicating an increased arm length • <u>Body Image task, BIT</u>^f * a single body part on a monitor as an anchor stimulus was showed, while participants are asked to judge the relative location of several other landmarks by clicking on the corresponding location on the monitor; a posteriori a perceived whole-body maps are reconstructed</p> <p>4. CONSCIOUS</p>

	<ul style="list-style-type: none"> • <u>matching body parts by function:</u> <p>^ point to pictured body parts that was most similar in function to a target body part</p> <ul style="list-style-type: none"> • <u>matching of body part to clothing and objects:</u> <p>^ point to pictured body parts that was most closely associated with a pictured item of clothing or tool (e.g. Object-Body Part Association task)</p>	<p>BODY IMAGE</p> <ul style="list-style-type: none"> • <u>template matching task</u> <p>^ participants have to indicate which observed hand (or body parts), among an arrays of hand (body parts) images stretched in various ways, from very long and slender to very squat and wide, is more similar to their actual hand (body parts) shape</p> <ul style="list-style-type: none"> • <u>line length task</u> <p>*/^ participants judged whether a line presented on the monitor was shorter or longer than different parts of their hands</p> <p>5. EMOTION-IN-BODY</p> <p>^ e.g. observation of images in which the body is a vehicle of emotional experiences (e.g. pain, affective touch, fear,...)</p>
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Table 2. A list of the principal tasks proposed to assess body representations in line with the main taxonomies (first row), adapted from (diadic view: ^aDe Vignemont, 2010; triadic view: ^bSchwoebel and Coslett, 2005, ^cDaurat-Hmeljiak et al. 1978, Raimo et al., 2019; somatoperception: ^dLongo, Azañón and Haggard, 2010, ^eSposito et al., 2012, ^fFuentes et al., 2013), but see the main text for more explanations and references. A further categorization is proposed between implicit (asterisks *) and explicit (circumflex accents ^) tasks.

Table 3

MULTISENSORY PROPRIETIES of PPS	DEFENSIVE PPS	SPATIAL REPRESENTATIONS based on a NEAR-FAR difference
<p>1. CROSSMODAL CONGRUENCY TASK: * participants are asked to discriminate the elevation of tactile stimuli administered either to a lower or an upper position on a body part (e.g. hand, but also head, the back and lower limbs), while ignoring visual (or auditory) cues presented at the same or a different elevation. Participants' responses are faster and more accurate when the tactile and the visual stimulus are presented at the same elevation, an effect termed, crossmodal congruency effect (CCE), that is more evident when visual cues are presented close to, rather than far from, the body.</p> <p>2. MULTISENSORY REACTION TASKS: * participants are required to reply as fast as possible to tactile stimulation on a body part, while concurrently task-irrelevant sounds or visual stimuli are presented either near or far from the stimulated body part. Results showed that responses to the tactile target were further sped up by sounds/visual stimuli (or even audio-visual stimuli) presented close as compared to far from the stimulated body part, suggesting that stimuli inside the PPS influenced tactile processing more strongly than stimuli outside the PPS.</p>	<p>1. HAND-BLINK REFLEX (HBR): * subcortical response, elicited by stimulation of the median nerve at the wrist and recorded from the orbicularis oculi. The strength of HBR varies as a function of the distance between the stimulated hand and the face of the participants, with higher responses when the hand is near rather than far from the face</p>	<p>1. LINE BISECTION TASK * when healthy participants draw a trait to divide into two parts a line in near space, they typically show a leftward bias (i.e. pseudo-neglect), but such bias shifts towards the right when the line is in far space. The point in space where this left-to-right deviation occurs has been used a proxy of the extent of PPS</p> <p>2. REACHABILITY JUDGEMENTS */^ participants are asked to give judgements about the possibility to reach an object in space, by providing explicit verbal answers or more indirectly by pantomiming a reach-to-grasp movement in response to the stimuli located near or far from the body</p>

Table 3. Short description of the main tasks proposed to assess peripersonal space (PPS), adapted from Serino 2019. Asterisks (*) indicate implicit tasks, while circumflex accents (^) underline explicit procedures. See the main text and Serino et al., 2019 for additional references.

Table 4

BODILY DISORDERS	DEFINITION
1. Alice in wonderland syndrome	Distorted awareness of the size, mass, shape of the body or its position in space (including macro/microsomatognosia and OBE)
2. Allochiria (or dyschiria) Allodynia	Mislocalization of sensory stimuli (tactile, visual, auditory) to the corresponding opposite half of the body or space
3. Allodynia	Pain due to a stimulus that does not normally produce pain
4. Anarchic hand sign	Unintended but purposeful and autonomous movements of the upper limb and intermanual conflict, see also alien hand syndrome (Hassan & Josephs 2016)
5. Anorexia nervosa	Eating disorder characterized by self-starvation
6. Anosognosia	Lack of awareness of one's deficits like hemiplegia
7. Asomatognosia	Failure of having a continuous sensation, feeling or judgment that one's body part (typically the impaired limb) belongs to the patient (Jenkinson et al., 2018; Romano & Maravita, 2019)
8. Autoscopy	Experience of seeing one's body in extrapersonal space
9. Autoprosopagnosia	Inability to recognize one's own face
10. Autotopagnosia	Mislocalization of body parts and bodily sensations
11. Body form agnosia	Deficit of recognition of body parts
12. Body Integrity Identity Disorder	Urge to be amputated of one's own perfectly healthy limb(s)
13. (BIID) Body-specific aphasia	Loss of lexical knowledge of body parts
14. Bulimia nervosa	Eating disorder characterized by recurrent binge eating, followed by compensatory behavior
15. Conversion disorder (hysteria)	Functional disorder with no organic cause
16. Cotard syndrome	Delusional belief that one is dead, does not exist, is putrefying or has lost one's blood or internal organs
17. Deafferentation	Loss of tactile and proprioceptive information
18. Depersonalization	Altered, detached, or estranged subjective experience
19. Dysmorphophobia	Distorted perception of one's self-appearance
20. Fading limb	Lack of awareness of the presence and position of the limb if not seen
21. Feeling of presence	Distinct feeling of the physical presence of another person or "being" in the near extracorporeal space although nobody is around (Brugger et al., 1997)
22. Finger agnosia	Inability to individuate and recognize the finger
23. Gerstmann's syndrome	Finger agnosia, agraphia, acalculia and left-right confusion
24. Heautoscopy	Visual hallucination of a double of oneself at a distance
25. Heterotopagnosia	Impairment in pointing to body parts on another person
26. Hyperalgesia	Increased response to a stimulus that is normally painful
27. Hypochondrias	Excessive somatic concern
28. Ideomotor apraxia	Inability to execute or carry out skilled movements and gestures
29. Interoceptive agnosia	Loss of pain feeling
30. Macro/microsomatognosia	Distorted awareness of the size of the whole body or of body parts (bigger or smaller)
31. Mirror sign	Inability to recognize one's own image in the mirror
32. Misoplegia	Hatred towards one's own body parts
33. Motion sickness (or kinetosis)	Vestibular balance disorder
34. Motor neglect	Under-utilization of one side of the body
35. Numbsense	Tactile deficit with preserved tactually guided movements
36. Out of the body experience (OBE)	Visual awareness of one's own body from a location outside the physical body
37. Pathological embodiment	A pathological form of embodiment towards another person's hand when this is located in a body-congruent position (Garbarini et al., 2015; Pia et al. 2020)
38. Personal neglect	Lack of attention towards one's side of the body

39. Phantom limb	Awareness of an amputated limb
40. Pusher syndrome	Postural deviation towards the contralesional side
41. Prosopagnosia	Deficit of face recognition
42. Somatoparaphrenia	The delusion that one's limbs belong to someone else (e.g. Vallar and Ronchi, 2009)
43. Supernumerary limb	Awareness of non-existent limbs
44. Tactile extinction	Lack of awareness of tactile stimuli on the contralesional limb during simultaneous bilateral stimulation

Table 4. A list of disorders interpreted as related to body representations, modified from De Vignemont 2010.

Table 5

DYADIC VIEW	TRIADIC VIEW	SOMATOPERCEPTION
<p>1. BODY SCHEMA: Dorso-parieto-frontal regions, “where” pathways</p> <p>2. BODY IMAGE: Ventral-parieto-temporal regions, “what” pathway</p>	<p>1. BODY SCHEMA: Bilateral, dorsolateral frontal (DLF) lobe, parietal cortices</p> <p>2. BODY STRUCTURAL DESCRIPTION: Associated with lesions involving putamen, anterior insula, temporal (i.e., middle and superior temporal gyrus extending to the TPJ), parietal (i.e., postcentral gyrus; angular gyrus, and supra- marginal gyrus) and frontal lobe (i.e., middle and inferior frontal gyri as well as precentral gyrus), extending to the surrounding white matter in right and left hemisphere</p> <p>3. BODY SEMANTICS: Left temporal lobe</p>	<p>1. SUPERFICIAL SCHEMA Parietal lobes, especially anterior parietal/TPJ</p> <p>2. POSTURAL SCHEMA Superior parietal and lateral intraparietal, especially in right hemisphere</p> <p>3. BODY MODEL Primary somatosensory and motor cortices, presumably parietal lobe</p> <p>4. CONSCIOUS BODY IMAGE PPC, especially in right hemisphere</p> <p>5. EMOTION-IN-BODY Anterior insula</p>

Table 5. Neural correlates of body representations proposed in line with the main taxonomies, adapted from (diadic view: De Vignemont, 2010; triadic view: Schwoebel and Coslett, 2005, Di Vita et al., 2019; somatoperception: Longo, Azañón and Haggard, et al. 2010; Tamé et al., 2021). See the main text and Longo, Azañón and Haggard, et al. 2010 for further references.

Figure 1

