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Review article

Relating different dimensions of bodily experiences: Review and proposition of an integrative model relying on phenomenology, predictive brain and neuroscience of the self

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ABSTRACT

How we mentally experience our body has been studied in a variety research domains. Each of these domains focuses in its own ways on different aspects of the body, namely the neurophysiological, perceptual, affective or social components, and proposes different conceptual taxonomies. It is therefore difficult to find one's way through this vast literature and to grasp the relationships between the different dimensions of bodily experiences. In this narrative review, we summarize the existing research directions and present their limits. We propose an integrative framework, grounded in studies on phenomenal consciousness, self-consciousness and bodily self-consciousness, that can provide a common basis for evaluating findings on different dimensions of bodily experiences. We review the putative mechanisms, relying on predictive processes, and neural substrates that support this model. We discuss how this model enables a conceptual assessment of the interrelationships between multiple dimensions of bodily experiences and potentiate interdisciplinary approaches.

1. Introduction

As human beings, we experience our body in multiple ways: as an object we can look at, as a source of feelings, as a social object embedded into cultural norms, as the primary sense of self, as a set of sensory receptors allowing perception of the external world, as a biomechanical support for action, etc. How the different dimensions of bodily experiences relate to one another is of paramount importance in many situations. For example, do individual with anorexia nervosa act as if they have an oversized body? Do the morphological changes occurring during adolescence alter the representation of body size and shape? Do my feelings about my body's shape influence my sensations and vice versa…?

This paper discusses how to study interactions between the motor, multisensorial, affective, cognitive and social aspects of bodily experiences. We first provide an epistemological perspective on the terminologies used in previous models (i.e. body schema and body image) and discuss their limitations. We argue that this question touches on one of psychology's central problem: the notion of the self in its sensory instantiation. We propose to draw from phenomenological approaches to merge conceptual accounts of different dimensions of bodily experiences with models of self-consciousness and phenomenal consciousness. We then review empirical and theorical work on bodily self-consciousness that highlights the role of sensory signals in bodily self-consciousness, self-consciousness and phenomenal consciousness. Based on this review, we propose a theorical model that allows conceptualizing the relationships between different dimensions of bodily experiences and the self. As such, it allows for an interdisciplinary approach on disorders implying both psychological and physiological aspects of bodily experiences like anorexia nervosa.

2. Multiple bodies in the literature and the shortcomings of the body image/body schema dichotomy in apprehending the multidimensional body

One difficulty in questioning the relationships between various dimensions of bodily experiences relates to the multiplicity of terms used in different research fields (Fig. 1) and their imprecision. An abundant literature has already reviewed the history of body-related concepts and the ambiguities in terminologies, notably with respect to the distinction between body schema and body image (see for example (Berlucchi and Aglioti, 2010; de Vignemont, 2010, 2020; Gallagher, 1986, 2005;

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Maravita, 2006). Here, we will focus on the limitations of these approaches for studying the relationships between multiple dimensions of bodily experiences.

In neuropsychology, movement science and cognitive science, most studies focusing on the body as a support for action refer to the seminal article published in 1911 by the neurologists Head and Holmes (see for example Assaiante et al., 2014; Holmes and Spence, 2004; Maravita et al., 2003; Martel et al., 2019). In this article, the authors proposed to call *schema* a combined standard, against which all subsequent changes in posture are measured before they enter consciousness. They distinguished it from the visual or motor *image* of the body that can be "recalled into consciousness" (Head and Holmes, 1911). As de Vignemont (2020) proposed, Head and Holmes can be considered as the pioneers of the representationalist approach, which bases bodily experiences on representations, defined as internal cognitive structures "that function to track the state of the body and encode it, that can misrepresent it and that can be decoupled from it". Besides, many recent studies in psychiatry, notably those dealing with eating disorders (see for example Gardner and Brown, 2014; Sattler et al., 2020), refer to the work Schilder (1935) who also used the term body image, which he defined as the "the picture of our own body which we form in our mind, that is to say the way in which the body appears to ourselves" (quoted in Gallagher, 1986). Schilder was the first to emphasize the role of the "unconscious libidinous elements" and "socially formed images of the body".

The model of two distinct representations, the body schema and the body image, has been regularly used in cognitive science and neuroscience (de Vignemont, 2010, 2020; Dijkerman and de Haan, 2007; Gallagher, 1986; Paillard, 1999; Pitron et al., 2018; Pitron and de Vignemont, 2017) and in eating disorders literature (see for exemple Keizer et al., 2013). Today, research investigating the relationships between different dimensions of bodily experiences often aims at characterizing interactions between body schema and body image (see for example Gadsby, 2017; Irvine et al., 2019; Pitron et al., 2018; Pitron and de Vignemont, 2017). But as definitions of these terms vary, closer either to the one from Schilder or to the one from Head and Holmes, it is difficult to get an integrative view of this research. Despite some consensus, the criteria used to distinguish between body image and body schema are disparate (de Vignemont, 2010). Concerning the consensual aspect, most studies associate the body schema to information about the physical properties that serve posture and action control. The term body image has often been used for experiences during which subjects direct their intention towards the body as a physical object and form a mental visual image of its size and shape. A sub-division into a "perceptual" component, an "affective" component, and a "cognitive" component of body image is also often used in research on eating disorders (Cash, 2004; Gaudio et al., 2014; Gaudio and Quattrocchi, 2012). The perceptual component is related to the identification, detection, and estimation of one's own body size; the affective component refers to the positive or negative feelings towards one's own body; and the cognitive component is defined as cognitive investment in body image or beliefs about the body's size and appearance (Cash, 2004). Yet the distinction between body schema and body image depends on the fields and questions of interest. Indeed, researchers have distinguished body schema from body image based on availability to consciousness (unconscious versus conscious), temporal availability (short-term versus long-term), format (sensorimotor versus visual) or functional role (action versus perception) (de Vignemont, 2010). So, referring to body image/ body schema relationship raises issues overlapping with a variety of research questions including the integration between bottom-up and top-down sensory processing, the relationship between unconscious process and access to consciousness, the overlap between action control and perception, etc.

A point of concerns deals with whether the body considered as the mean to perceive the external world refers to body schema or body image. On one hand, Gallagher (1995) pointed that the body schema "corresponds to the body as it functions to make perception and action possible". Only the body as it is consciously perceived (and not used to perceive) and visually represented is linked to body image. On the other hand, other authors from the representationalist approach have

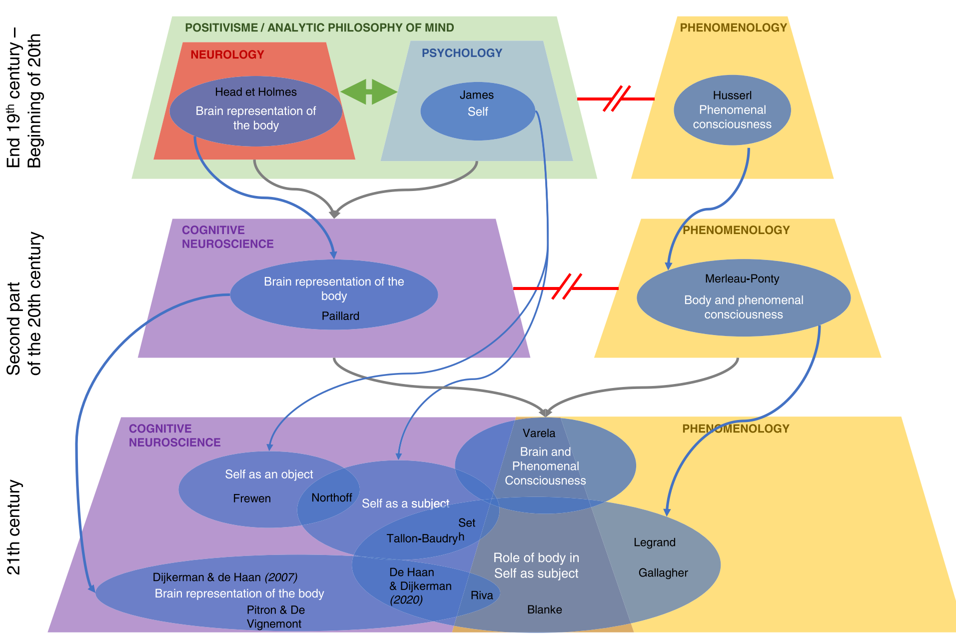

Fig. 1. ***Schematic flow chart placing the main theoretical frameworks discussed in the article.*** At the turn of the 20th century, psychology moved away from introspective methods and promoted a scientifically based examination of the mind and behaviour, aligning with the principles of positivism. The work of Head and Holmes addressed the mind-body relationship from a neurological perspective while dialoguing with psychologists. Phenomenology developed in parallel, remaining distant from approaches investigating the representation of the body (de Vignemont, 2020; Smith and Thomasson, 2005). The emergence of embodied and embedded approaches at the end of the 20th century marks an explicit rapprochement between phenomenology and cognitive science (Varela, 1996; Varela et al., 1993), concomitant with expansion of the study of neurophysiological correlates of phenomenal consciousness. The study of implicit consciousness of being a body, what we call bodily self-consciousness, took a new turn with the landmark publication of the first paper on the rubber-hand-illusion in 1998 (Botvinick and Cohen, 1998). This study sparked ongoing research on the place of the body in the self as a subject. Representationalist approaches also delved into this realm by seeking the brain's representation of the body. Also, with advances in neuroimaging, an increasing number of studies aimed to identify the brain bases of the self-as-a-subject as well as of the self-as-an-object. This overview is however simplified and reductive. For example, Schilder's ideas were influenced by both Head and Holmes's concept of body schema and by Husserl's ideas.

postulated that the dimension of the body that is used to perceive sensory stimulations pertains to the body image (de Vignemont, 2010; Dijkerman and de Haan, 2007; Pitron and de Vignemont, 2017). They mapped the body schema/ body image dichotomy to the two-pathways model of sensory information processing according to which information is processed in parallel by different brain circuits for action (e.g., planning hand movements; dorsal pathway) and for perception (e.g., object recognition; ventral pathway), respectively. The body schema would depend on the dorsal pathway and be related to action only (not perception), and the body image would depend on the ventral pathway and be related to perception (Dijkerman and de Haan, 2007). These two conceptions can lead to different interpretations. Indeed, whereas a distorted perception of passive touch would imply a body schema distortion following Gallagher's definition, it would imply a body image distortion according to de Vignemont's definition.

Elaborating from this position, Pitron and colleagues (Pitron et al., 2018; Pitron and de Vignemont, 2017) proposed a theorical model in which both body schema (action-related) and body image (perception-related) are based on multisensory signals as well as on *prior knowledge*. Each representation could be one prior among others to build the other one. These two dimensions of bodily experiences would thus influence each other mutually and the relationship between the two could be explained by a *co-construction*. For example, a distorted perceptual body image could be a prior for updating the body schema, which would therefore also be distorted. Such a strict separation between action and perception (in general and in the case of the body) is however questionable. From a phenomenological point of view, it is difficult to imagine a body image that does not take into account the fact that the body is a support for action. From a neurophysiological point of view, the separation of functions between the dorsal and ventral pathways is challenged by the growing evidence of extensive crosstalk between the two pathways (rev. in de Haan and Dijkerman, 2020). As a result, the idea that there are two distinct representations based on functional properties supported by distinct brain circuits is questioned. Therefore, it remains unclear whether studying the multidimensional body in terms of body schema/body image relationship can hold.

Additionally, independently of the distinction used, it is challenging to empirically isolate the body schema from the body image. For example, one popular task used to study body schema, and its potential distortion, consists in asking participants to judge the smallest aperture between two sliding doors they could pass through (e.g., Irvine et al., 2019). Since this task is related to action, in the sense that it is resolved by simulating the action of walking through, authors using functional criteria to differentiate body schema and body image consider that it engages the body schema. But one may argue that this task also implies the subject's intention to be directed towards the size, the width and shape of the body; thus, it may also require to appraise the body as an object, and therefore body image. This task is thus limited if one wants to understand the relationship between action-related processes and other dimensions related to consciousness of body size and shape. Nevertheless, from a theorical point of view, interpreting this task as specifically assessing the body schema is coherent with Schwoebel and Coslett's (2005) who argued that we can be conscious of the body schema during motor simulation tasks. But this body schema, which is here consciously accessible, would therefore need to be separated from Gallagher's body schema, which is "subconscious" and "unowned" (Gallagher, 1986). Thus, Schwoebel and Coslett (Schwoebel and Coslett's, 2005) are talking about a bodily experience that is different from Gallagher's one. In other versions of the aperture task, participants have not only to imagine but also to execute the action by walking through door-like openings varying in width (Metral et al., 2014). But these versions do not allow isolating the body schema either: they involve elements related to body image as they imply directing intention towards the body size and shape and should thus also be differentiated from Gallagher's body schema, which is "extra-intentional". Other tasks used to evaluate body schema consist in asking the participant to point to a touched or named body part. But these tasks are also not exclusive, as they require a memory of the body size and relation between the pointing hand and the touched body part, neither exhaustive as they focus on only one part of the body (de Vignemont, 2010).

With respect to body image, one task sometimes deemed specific is to ask participants to draw themselves (Guez et al., 2010) or someone of the same body size (rev. in Havé et al., 2021). But here again one may argue that this task mobilizes having an accurate internal representation of body parts topology, which typically concerns body schema. Other tasks, referred to as "body size estimation tasks", consist in asking participants either to select the body size they estimate to be their own among a set of individualized weight-distorted photos, videos or virtual avatars representing their body (depictive methods), or to estimate their body parts size on a spatial scale (metric methods) (Mölbert et al., 2017). While these tasks undoubtfully tap into body image as defined by representationalist approaches, it is not clear however to which dimension of body image they are specific. Indeed, some authors claim that errors are unlikely to reflect purely a disturbance in the perceptual domain as one cannot adequately ensure "that cognitive and emotional aspects of body image do not 'contaminate'" how the task is performed (Mussap and Salton, 2006; see also Cornelissen et al., 2019; Legrand, 2010; Mölbert, Klein et al., 2017). As pointed by Gallagher, many results from body-image tests "bear a closer relationship to [the subjects'] attitudes to treatment or the experimenter than to [the subjects'] perception of their bodies" (1986). Furthermore, in patients (Cash and Deagle, 1997), as well as in healthy populations (Longo and Haggard, 2012), results from the depictive and metric methods do not correlate, casting doubts on their potential to measure the same entity. Longo et Haggard (Longo and Haggard, 2012) also reported a distortion of the hand size estimation that was intermediate between the real size and the level of distortion in localization (measured in another task); they concluded that at least the metric version of the body size estimation task involves not only a perceptual (visual) representation of the hand, akin to body image, but also some somatosensory representations, akin to body schema.

Many empirical studies combined several of these tasks, providing valuable information on the relationship between different dimensions of bodily experiences (Campione et al., 2017; Guardia et al., 2012; Irvine et al., 2019; Keizer et al., 2013; Lautenbacher et al., 1993; Longo and Haggard, 2012; Metral et al., 2014; Salomon et al., 2012). But due to the divergent definitions of the concepts these studies manipulate, it is ultimately impossible to integrate their findings into a comprehensive model based on the sole dichotomy between body schema and body image.

In sum, even if the concepts of body schema and body image are relevant for some research fields, the definition, and criteria for differentiating the two, as well as the experimental paradigms to study them, are not consensual. Consequently, the interrelation between body schema and body image is also ill-characterized. Therefore, it becomes challenging to connect studies addressing one or another approach and to understand the relationships between multiple dimensions of bodily experiences.

Alternative models have been proposed. Some added other categories of representation (Longo, 2016; Schwoebel and Coslett, 2005). Longo (2016) proposed for example a taxonomy with six representations (the body image, the body schema, the superficial schema, the body model, the body as a distinct semantic domain and the structural body). But the question of how many body representations exist seems unsolvable, in view of the variety of ways to experience our own body (de Vignemont, 2007; Kammers et al., 2010). These models are thus restricted to address only a specific question or pathology; they do not allow integrating the various dimensions of bodily experiences comprehensively. Other authors have proposed that a supramodal entity called *long term body image* (Gadsby, 2019; O'Shaughnessy, 1998) or *body matrix* (Melzack, 2005; Moseley et al., 2012) would determine and influence the subordinate dimensions. Recently, Riva (2018) presented a detailed model in which the supramodal representation *body matrix* contains stored information not only from perceptual experiences (i.e., the size and the shape of the body) but also from conceptual attributes (i.e., the meaning attributed to the body), and episodic memory (i.e., the key autobiographical events related to the experience of the body). This stored information would be used to calibrate multisensory inputs. Although the notion of body matrix incorporates the emotional and perceptual aspects of the body with its neurophysiological dimensions, it is still limited when it comes to integrating the vast research presented above, more particularly differentiating what is part of consciousness and what belongs to unconscious processes or differentiating what is intentional or non-intentional (see after). de Haan and Dijkerman (2020) also called into question the idea of two separate body representations based on two independent pathways. They proposed a model of somatosensory processing in the brain based on five different networks involved in separate subfunctions ("haptic object recognition and memory", "body perception", "body ownership", "affective processing", and "action-related somatosensory processing"). The authors emphasize however that these networks are highly interconnected and multimodal in nature. But these models are still incomplete when it comes to describing an integrative view of the bodily experiences. In particular, with respect to sensory processing, a larger part should be given to interoception, vestibular system and sense of movement. Concerning the conceptual level, the social and emotional aspects of experience of having a body, as well as non-bodily self-related processes or the perception of others' bodies are not accounted for. To address these limitations, we propose a new model based on an integrated and interdisciplinary approach drawing from a conceptual clarification from phenomenal approaches as well as recent findings from studies on bodily self-consciousness, self-consciousness and phenomenal experience.

3. Organizing and defining conceptual boundaries of the different dimensions of bodily experiences through the lens of phenomenology

An author frequently cited in the domain of body investigation is Merleau-Ponty. The French philosopher used the term *body schema*, which he defined as a set of sensorimotor laws built through experience — rather than a sensorimotor representation — that constrain the perceptual and motor experiences of the body (Merleau-Ponty, 1945). As we already stated, this concept can easily lead to miscommunication and complexify the understanding of the multiple dimensions of bodily experiences. The phenomenological approach, however, is useful for elucidating the relationships between different dimensions of bodily experiences since it emphasizes subjectivity and *experience*. In fact, while different research fields, or even individual studies, have used various terms and sometimes idiosyncratic definitions to investigate the body, what is common to all these situations is the experience of the subject, the phenomenal consciousness, the "it feels like something to" (Nagel, 1974). As defined by Chalmers (1995), "there is something it is like to be a conscious organism. This subjective aspect is experience." By examining where in the experience, different studies place the body, and which body dimensions they consider (Fig. 2), we hope to expose conceptual links between definitions of bodily experiences as used in different disciplines and traditions. We will here restrict our analyses to experiences involving a "usual" state of consciousness (not meditating or sleeping for example).

Our starting point (see Figure 2) comes from a philosophical tradition (Husserl, 1989 cited by Legrand, 2006a) put forward by the psychologist and philosopher (Legrand, 2007) who emphasizes that any conscious experience can be defined by an object-directedness (intentionality) and by a subject-relatedness (first-person standpoint). Intentionality refers to the fact that consciousness is always directed towards an object, be it material, conceptual or an event. The content of subjective experience refers to phenomenal consciousness and is present only in the subject, it exists only for her/him (see Fig. 2 inside the pink circle). In our schema all elements inside the pink circle represent the content of experience (by definition, unmaterial), whereas all elements outside the pink circle are neurophysiological events — are part of the physical or objective world – and shape the content of phenomenal consciousness. In line with phenomenological approaches that emphasize the distinction between the external world that exists through consciousness — i.e., through a subject — and the objective external world, we place the objects of intention *in* the subject's consciousness. Thus, in this schema, the body can be placed first in the pink circle, i.e., as an *intentional object* of one's conscious experience (see Fig. 2. B). This is for example — but not only, — when we think about or look at it, as we could do for any other physical object present in the external world. Like for any object, the experience of the intentional-object body and the physical-object body are not isomorphic. For example, when anorexic patients turn their intention towards how their body looks like, pondering its size and shape, they may experience it bigger than it is in the objective external world (see below for more debate on this point).

From this basic definition of experience, let's delve into what constitutes an experience. As explained by Legrand (2006a, 2007), when my intention is directed towards an object, for example when I look at a tree or when I look at myself in the mirror, I am conscious of the object of my intention (the tree or the physical image of my body), but I am also implicitly conscious of the *I* of this experience — even if my intention is not turned towards this *I*. I am implicitly aware that I am a subject, that I exist as a self, that the tree is seen by somebody, that I am able to see my body's reflection. This sense of self is defined as the minimal or pre-reflexive *self-consciousness*. A pre-reflexive state, which is minimally or elusively conscious (Legrand, 2007), is not to be to be confounded with an unconscious process. The former, contrary to the latter, is *in* the sphere of consciousness, even if it is not the intentional object. According to many authors with a phenomenal approach, pre-reflexive and implicit *self-consciousness* serves as a transparent foundation for all other experiences; it structures them and influences their quality (Legrand, 2006a). This might be related to the proposition that a baseline internally generated brain activity conditions perception and cognition in relation to the subject (*self-related processing*) (Northoff, 2016). We therefore propose implicit self-consciousness process as a basis of phenomenal consciousness in the model we propose in part V (see also Figure 2.C).

The neuroscientist Blanke and the philosopher Metzinger (Blanke and Metzinger 2009) relate pre-reflexive self-consciousness to the pre-reflexive sense of being an bodily subject (see also Faivre et al., 2015; Gallagher, 2005). This is in line with a philosophical tradition that points that any phenomenal experience presupposes the experience of the body lived in its subjectivity (Legrand, 2006b), or a "lived body" according to Merleau-Ponty (1945). This implicit and pre-reflexive experience of being the subject of a given experience can also be referred to as *bodily self-consciousness* (Blanke et al., 2015; Legrand, 2006b, 2007; Lenggenhager et al., 2007; Ronchi et al., 2018). Bodily self-consciousness is therefore also a foundation for phenomenal consciousness (see Fig. 2C.). Bodily self-consciousness is often defined as being constituted by four feelings: ownership (the feeling that one body is one's own), agency (the feeling of self-generating action), first-person perspective (the feeling that "I see the world from here"), and self-location (the feeling that I am in my body) (Blanke, 2012). Since the beginning of the 21st century, a broad research field has been studying the role of multisensory inputs in the emergence of bodily self-consciousness. The body is analyzed in its neurobiological aspects, as a set of sensorimotor inputs (see Fig. 2. C). Within this field, a number of authors, based on theoretical and empirical grounds, discuss the fact that the integration of these bodily signals also constrains the content of phenomenal consciousness (Faivre et al., 2017a and 2017b; Tallon-Baudry et al., 2018). In this research framework, the neurophysiological dimension of the body structures and influences all experiences and mental states, including those directed towards the self as

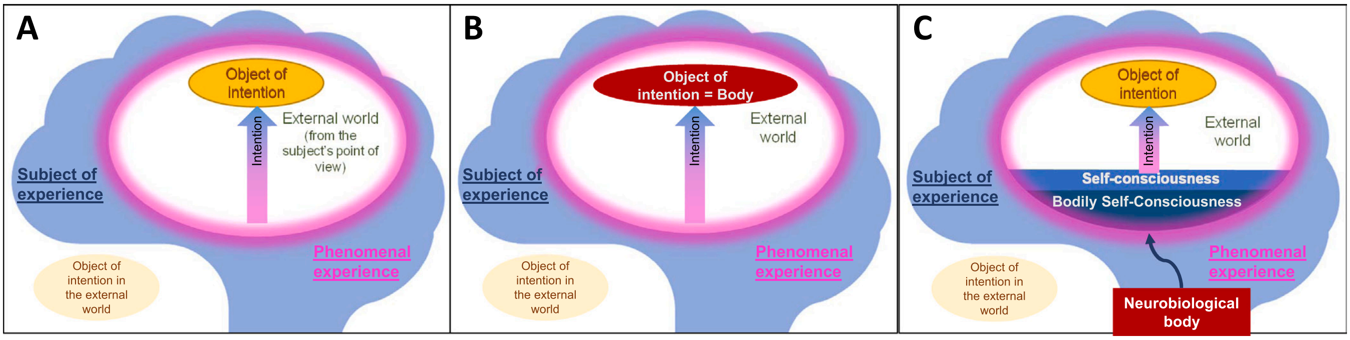

Fig. 2. ***Place of the Body in Different Dimensions of Experience.***
A. Experience from a phenomenological approach. B. The place of the body in experience for many clinical and cognitive psychology studies: the body is the intentional object of consciousness. C. The place of the body in experience according to studies dealing with bodily self -consciousness, self-consciousness,and perceptual consciousness: the body is constitutive of the subject, shaping the content of phenomenal experience.

an object (Qin et al., 2020).

Here it seems necessary to insist on the differentiation between the content of subjective experience and the mechanisms sustaining this experience. When we use the term "body", in some cases we refer to the body as part of the *content* of phenomenal consciousness: the body is then in the consciousness' sphere, as the intentional object of experience (for example when I create a mental representation of my body size) (body in Fig. 2. B) or as the non-intentional, implicit and pre-reflexive bodily self. In other cases, the body is just part of the *mechanism* that sustains or shapes the content of consciousness (body in Fig. 2. C). Thereby, the content of phenomenal consciousness when we experience the body as an intentional object needs to be clearly distinguished from the multimodal and multi-level mechanisms supporting this experience. This conceptual distinction becomes harder when talking about experiences during which intention is directed towards the neurophysiology of the body – the sentient and acting body. We think here of tasks directing intention towards one's own body moving or towards a mental representation of movement, as for example in the aperture judgment task described above. In these situations, the intentional content of phenomenal consciousness, the mentally represented sensations and movements — what Schwoebel et Coslett (Schwoebel and Coslett, 2005) called body schema — is distinct from the set of neurophysiological processes sustaining this experience — composed in part of what Gallagher called body schema (Gallagher, 1995). Firstly, in this situation, one can have a mental picture of one's body moving but one has no access to the neurophysiological mechanisms of sensorimotor integration (Gallagher, 1986, 1995). Secondly, the neurophysiological activity enabling the mental image involves multimodal and multi-level processes that are not restricted to sensorimotor inputs but also include affect, knowledge and beliefs related to the self and the bodily self (Guillot and Collet, 2005; Reed, 2002). Of course, the intentional content and the underlying sensorimotor mechanisms are not independent. It is well accepted for example that imagined and executed actions share some neural substrate (Decety, 1996). In this sense, the content of experience can inform partially about the neurophysiological mechanisms in question. But the content of consciousness does not tell the whole story, nor only the story, of sensorimotor inputs integration in the previously cited tasks.

Finally, as we will see in the following part, all experiences, including those during which intention is directed towards our body as an object, implies multilevel and multimodal mechanisms. The content of phenomenal consciousness is always shaped by multisensorial bodily inputs as well as high-level mechanisms. Recent findings from studies investigating phenomenal consciousness, self-consciousness, and bodily self-consciousness, in particular those using illusions, allow for a deeper comprehension of these mechanisms. Starting from research showing that multisensorial bodily inputs and higher-level mechanisms shape bodily self-consciousness, we attempt to incorporate all these findings into a single comprehensive model.

4. Review of evidence that multisensorial bodily inputs and higher-level mechanisms are involved in bodily self-consciousness

Since Botvinick and Cohen's seminal article (Botvinick and Cohen, 1998), illusions paradigms have become classic tests to study bodily self-consciousness. The authors induced an illusory feeling of ownership over a rubber hand by putting it on a table in front of the subject, hiding her real hand, and stroking simultaneously the rubber and real hand (Rubber Hand Illusion). About 10 years later, based on the same visuo-tactile congruence principle, the full-body illusion paradigm was used to induce the illusory feeling of ownership and agency over a virtual or mannikin's whole body presented in third person perspective (Aspell et al., 2013; Lenggenhager et al., 2007) or in first person perspective (Maselli and Slater, 2013; Petkova, Björnsdotter et al., 2011; Petkova and Ehrsson, 2008). In these studies, the virtual body (or manikin body), presented via a virtual reality device (or head-mounted displays connected to a pair of cameras mounted on the head of a manikin), is perceived as being the source of the associated bodily sensations and as being the subject's own body. The feeling of body ownership is stronger in first person than in third person perspective (Petkova et al., 2011). Initially, full-body illusions were induced via visuo-tactile congruent stimulations (Petkova and Ehrsson, 2008): observers experienced tactile stimulation on their body and simultaneously saw the mannikin or avatar being touched at the corresponding location on the body. Subsequent studies reported that visuo-proprioceptive or visuo-motor (Maselli and Slater, 2014; Peck et al., 2013) stimulations could also induce the illusion. Interestingly inducing an illusion on a body-part, namely the hand, creates a drift in the perceived location of the hand as well as a shift in the perceived orientation of the body, demonstrating a tight link between body-part and full-body ownership feelings (Olivé and Berthoz, 2012). Combining full-body ownership illusion with galvanic vestibular stimulation, Preuss and Ehrsson (2019) revealed that vestibular inputs also influence the strength of the illusion, and are thereby involved in bodily self-consciousness. Proprioceptive signals were also found to have a role in bodily self-consciousness since proprioceptive noise (induced by muscle vibration) modulates self-identification with the virtual body (Palluel et al., 2011). Banakou et al. (2013) and Peck et al. (2013) also reported that first-person perspective full-body ownership illusion over an avatar, induced by synchronizing virtual and real body movements, is extinguished when the virtual body moves asynchronously with respect to the subject's real movements. The role of interoceptive signals has also been reported (rev. in Park and Blanke, 2019; Seth, 2013; Seth and Tsakiris, 2018). For instance, a virtual body flashing in synchrony with the subject's respiration pattern (Allard et al., 2017) or heartbeat (Aspell et al., 2013) induced a stronger illusion compared to a body flashing asynchronously. This effect was stronger in people with a lower capacity to perceive their interoceptive sensations (Tsakiris et al., 2011). Coupling neuroimaging and full-body illusion, Park et al. (2016) showed that transient modulations of neural responses to heartbeats covary with the illusion. This suggests that central interoceptive inputs integration also supports bodily self-consciousness. In sum, illusions reveal that bodily self-consciousness results from the integration of multiple bodily signals: visual, tactile, vestibular, proprioceptive and interoceptive (see reviews in Kilteni et al., 2015; Park and Blanke, 2019; Ronchi et al., 2018; Tsakiris, 2017). Disorders of bodily self-consciousness, like autoscopic phenomena (the subjective mental experience in which the person has the impression of seeing a duplicate of their own body in out-of-body space), are considered to result from an inability of the brain to process multisensory integration (Blanke and Arzy, 2005; Lopez et al., 2010; Lopez and Elzière, 2018).

Knowledge, beliefs and affects about the body as a physical or physiological object also influence bodily self-consciousness. Reviewing the modalities and conditions for inducing body-ownership illusions, Kilteni et al. (2015) proposed that *body models*, defined as mental representations of the body that contain generic information about the visual, postural and structural properties of the human body, respectively, contribute to creating bodily self-consciousness. For instance, the rubber hand illusion vanishes when the object seen in place of the hand is not a plausible representation of a hand but a wooden block with carved wrist and fingers (Tsakiris et al., 2010). The extent to which the discrepancy between the seen body and the subject' s actual body can impact the strength of the illusion remains a matter of debate, however. Some authors reported, for example, that the size of the rubber hand modulates the apparition (Pavani and Zampini, 2007) or the strength (IJsselsteijn et al., 2006) of the illusion and concluded that specific cognitive mechanisms may constrain the illusion, whereas other authors did not report significant differences when using a small (e.g., hand size of a small child) or large hand (e.g., hand size of a tall man) (Heed et al., 2011). Similar results are observed at the whole-body level: several studies have reported ownership illusion towards artificial bodies of different sizes (Banakou et al., 2013; van der Hoort et al., 2011), sexual characteristics (Slater et al., 2010; Tacikowski, Fust et al., 2020) and shapes (Normand et al., 2011; Preston and Ehrsson, 2014, 2016; Provenzano et al., 2019; Rubo and Gamer, 2019). The illusion appears however more easily (with less stimulation) when the seen body matches the actual features of the subject' body (similar shape, skin tone and position) (Maselli and Slater, 2013), suggesting that information related to the physical characteristics of one's own body is mobilized for bodily self-consciousness.

Additionally, the strength of the rubber hand illusion is positively associated with scores on body dissatisfaction scales (Kaplan et al., 2014), suggesting that affects and beliefs related to the body as a physical object are also associated with bodily self-consciousness. Other factors, which we regroup under the term *non-bodily self* factors, are also associated with the likelihood and strength of the illusion and are thus likely to be linked with bodily self-consciousness. For instance the rubber hand illusion correlates with temperament (Kállai et al., 2015), the presence of dissociative subtype of post-traumatic stress disorder (PTSD) (Rabellino et al., 2016), a high index on "Perception and Thinking problem" domain of Rorschach test (Burin et al., 2019), and schizotypal personality disorder (Thakkar et al., 2011). Interpersonal skills such as high empathic traits (Asai et al., 2011; Mul et al., 2019; Seiryte and Rusconi, 2015) and high index on the "Self-consciousness and Other Representation" domain of Rorschach test (Burin et al., 2019) are also associated with a stronger rubber hand illusion. During experiences of embodiment towards a virtual avatar seen from first person perspective, an internal locus of control (i.e., when people believe that they have control over the outcome of events in their lives, as opposed to external forces beyond control) is positively correlated with a higher sense of agency, whereas an external locus of control is positively correlated with a higher body ownership feeling (Dewez et al., 2019). All these *non-bodily self* factors are associated with interindividual variability in bodily self-consciousness. Interestingly, knowledge about the physical world in general, and individual perceptual biases also influence the illusion: for instance, the visual influence of the frame in the rod-and-frame test correlates with the strength of rubber hand illusion (David et al., 2014).

5. Proposition for an integrative model

5.1. The model

5.1.1. Multiple levels organized in a generative model of bodily self-consciousness

The findings reported above highlight that both multisensory inputs and higher-level mechanisms related to the bodily and non-bodily self constrain bodily self-consciousness, as assessed by illusions. Building from these findings and theoretical multi-level descriptions of self-consciousness (Gallagher, 2005; Riva, 2018; Seth and Friston, 2016; Tsakiris, 2017), we propose here a simple classification of the different components constraining bodily self-consciousness. We distinguish different levels ranging from unimodal sensation (visual, tactile, vestibular, interoceptive, proprioceptive) to multisensory integration (or body mereology), to levels related to body as a physical object, up to more abstract representations of self that we qualify as non-bodily self and, to social and external world related levels (Fig. 3). Together, these levels constitute a global dynamic generative model, which integrates information from each level and sustains bodily self-consciousness.

5.1.2. Bayesian and predictive coding model of bodily self-consciousness

The way bodily self-consciousness, or some components of it like ownership feeling, can emerge from these multi-level factors has been explained in the context of predictive coding and Bayesian approaches of brain functions (Apps and Tsakiris, 2014; Chancel et al., 2022; Fang et al., 2019; Kilteni et al., 2015; Preuss Mattsson et al., 2022; Samad et al., 2015; Seth, 2013; Tsakiris, 2017). In the Bayesian probabilistic framework, the sense of one's own body is constructed through a process of "causal inference" in which the brain infers the probability that sensory signals share a common cause taking into account spatial proximity, simultaneity, temporal correlation, sensory uncertainty, and prior perceptual experiences (Samad et al., 2015; Fang et al., 2019; Chancel et al., 2022). According to predictive coding theories, the way we perceive and experience the world and the self relies on the brain ability to interpret incoming inputs based on predictions. Schematically, once noisy bottom-up multisensory inputs arrive from the periphery, the brain uses stored predictions to decode these signals and to infer the most likely features of objects and events at the origin of these signals. The content of experience is thereby specified by these organized generative processes that make top-down *predictions* about the causes of sensory signals. These predictions are based on priors about the body, the self and the world (Friston, 2009; Seth, 2013; Tsakiris, 2017). Inputs from the periphery are compared to these probabilistic predictions. At each level of the model, if predictions stored in priors do not match with incoming information, then *prediction errors* are computed. These prediction errors can be minimized either by updating the different predictions, or by performing actions to bring sensory inputs closer to predictions (active inference) (Seth, 2013). Actions here could be voluntary but also involuntary or autonomic (Seth and Tsakiris, 2018). Whether predictions are updated or whether actions are performed to change the sensorial inputs depends on precision weighting. Indeed, both predictions and incoming inputs vary in precision and are thus more or less reliable. Signals that are the most precise receive a higher relative weight (Apps and Tsakiris, 2014; Tsakiris, 2017). So, when sensory inputs are not reliable — i.e., are noisy — prediction errors will be minimized through active inference. On the contrary, if sensory inputs creating prediction errors are highly reliable, prediction errors will

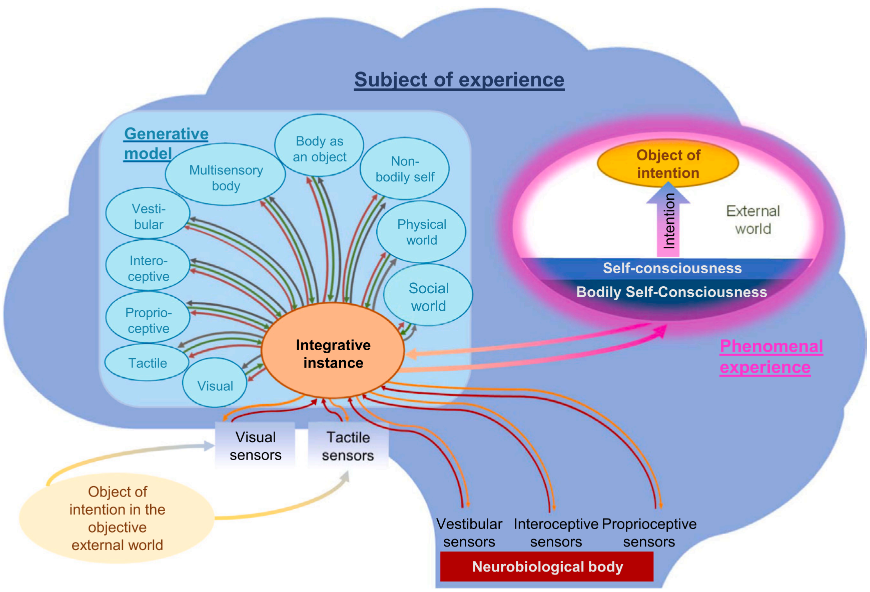

Fig. 3. ***Integrative Model for Conceptualizing Different Dimensions of Bodily Experiences and their Relations***. Multisensorial inputs and high-level brain mechanisms shape the content of phenomenal consciousness, including bodily self-consciousness and self-consciousness, based on predictive coding theories. Priors (blue circles) store probabilistic predictions about multisensorial inputs, the body mereology, the self and the world. Afferent multisensorial inputs (red arrows) are compared to these predictions. If sensory inputs do not match predictions, prediction errors (green arrows) arise.They are minimized by updating priors composing the model (grey arrows) and/or by active inference (orange arrows). This dynamic system conditions phenomenal experience. Reciprocally, subjective experience influences the dynamic and modifies the priors.

be minimized through an updating of predictions. According to this theory, the brain learns through time and experience the best set of relative weights to assign to the different incoming inputs and to the different predictions. This weighting rules are stored in an integrative instance constantly updated. Thereby, the content of phenomenal consciousness is shaped by — and at the same time influences — a dynamic model composed of priors, weighting rules and neurophysiological inputs (Fig. 3).

For example, Tsakiris (2017) explains that during the rubber hand illusion, visual and tactile inputs suggest that what I am looking at is my hand whereas proprioceptive inputs suggest that my real hand is not exactly where I see it. This conflicting information between different sources of unimodal bottom-up information does not fit the top-down predictions of the multisensory priors; prediction errors are created. These prediction errors may be minimized through two kinds of inference. Firstly, some priors may be updated in the organized generative model. This may result in a change in the phenomenal content, creating the feeling that this rubber hand is mine. Secondly, active inference may change input sampling and the way my brain integrates inputs from my hands. This would explain why ownership illusion over a rubber hand with a larger or smaller grip aperture impacts grasping movements (Kammers et al., 2010) or why body ownership led to decreases in tactile sensitivity in my real hand (Ataka et al., 2022) and body (Aspell et al., 2013). In contrast, if the illusion does not occur, this indicates that the priors related to multimodal, bodily, and non-bodily self are precise and robust enough and/or that the integrative instance correctly attributes a high confidence to proprioceptive inputs and low confidence to visual input. The frequency and strength of the illusion is thus inversely correlated with the precision and robustness of the whole model (Tsakiris, 2017). In this view, illusion paradigms can inform about the robustness of the whole organized generative model sustaining phenomenal consciousness.

By integrating many dimensions of the self and the body, namely unimodal bodily inputs, multisensorial body, body as an object, non-bodily self, physical and social world related parameters, and by relating them to phenomenal consciousness, this model can account for a large number of empirical results relating different dimensions of bodily experiences. For example, active inference, changing sensorimotor signals and thereby motor commands, would explain why ownership illusion of a virtual body more corpulent than the participant's actual body increases safety distances with the walls when walking (Rubo and Gamer, 2019). Active inference during full body illusion could also modulate corollary discharge during motor preparation and decrease pain perception (Hänsell et al., 2011) (see Pyasik et al., 2022 for a recent review on how full body ownership illusions influence action execution, pain and body perception). Changes in reports of own-body or self representational features could result from prediction updating. For instance after induction of the rubber hand illusion, participants perceive their own hand as significantly more similar to the rubber hand (Longo et al., 2009) or significantly smaller (Carey and Preston, 2019); illusory ownership of a slimmer body decreases the perceived body width and increases subjective body satisfaction (Preston and Ehrsson, 2014); experiencing body ownership of a child avatar promotes self-attribution of child-like attributes (Banakou et al., 2013).

Also, the implicit experience of being a bodily self relies on a dynamic process that permanently compares upcoming inputs to stored priors and permanently updates these priors. Transient embodiment feeling during asynchronous visuo-proprioceptive stimulation (in full-body illusions paradigms; Keenaghan et al., 2020) could reflect the time needed to compute prediction errors arising from the incongruent multisensorial stimulation and to update the priors (i.e transform 'the body I see is mine' vs 'the body is not mine'). The tolerance to some delay between visual and tactile stimulation for experiencing the ownership feeling could reflect a low weight to the error precision, that could also generalize to other phenomena requiring temporal integration (Costantini et al., 2016).

5.2. Evidence that bodily signal inputs and higher-level mechanisms are implicated in self- and phenomenal consciousness

Considering on one hand the role of bottom-up multisensory signals and of an organized brain model for bodily self-consciousness, and, on the other hand, the view of bodily self-consciousness as a foundation for self-consciousness and phenomenal experience, one might hypothesize that mechanisms for bodily signals prediction also underlie self-consciousness and phenomenal consciousness in general. A number of empirical studies tend to support this idea.

For example, Babo-Rebelo et al. (2016) reported that heartbeat-evoked responses in the precuneus and posterior cingulate cortex covary with the self-relatedness of spontaneous thoughts during mind-wandering, indicating a relationship between interoception and pre-reflexive self-consciousness. Also, when participants were asked to imagine themselves (from a first-person perspective) or a friend (from a third-person perspective) in various scenarios, the amplitude of heartbeat-evoked responses differed (Babo-Rebelo et al., 2019). This is in line with Tallon-Baudry et al., (2018) 's review that highlights the importance of central processing of interoceptive inputs for adopting a first-person perspective (see also Seth, 2013; Seth and Tsakiris, 2018). Likewise, meta-cognition, a form of self-consciousness, is influenced by sensorimotor signals as evidenced by the fact that evoking sensorimotor conflicts while participants perform a perceptual task impacts confidence judgments on performance (Faivre et al., 2020).

These predictive processes impact more generally how we experience the external world (Harris et al., 2015; Park and Tallon-Baudry, 2014; Pyasik et al., 2022). Park et al. (2014) reported for example that spontaneous fluctuations in neural responses to heartbeats predict visual detection of near threshold stimuli. Faivre et al. (2017a) and (2017b) showed that in a rubber hand illusion paradigm, participants perceived a lateral drift of a visual image projected on their hand towards the rubber hand only when the rubber hand was embodied, indicating that multisensory integration impacts the way subjects perceive external stimuli in peripersonal-space. van der Hoort et al. (2011) and Banakou et al. (2013) also demonstrated that body ownership illusion over a body with a different size influences the perceived size of external objects. Besides, induction of unusual bodily self-consciousness experiences, investigated through ownership illusions over avatars from different ethnic or social group, might modulate the affective and social content of phenomenal consciousness related to others (Banakou et al., 2013; Farmer et al., 2014; Maister et al., 2015; see Pyasik et al., 2022 for a review on how full body illusions influence perception of external object and social cognition).

Lastly, bodily signals inputs seem to impact phenomenal content also when the object of consciousness concerns non-bodily aspects of the self. Tacikowski et al. (2020) reported for example that an illusion of body swapping influences self-related concepts: after embodying a friend's body, participants rated their own personality characteristics as more similar to how they previously rated their friend's personality (see also Pyasik et al., 2022). This is line with models that put forward the role of bodily inputs on self-related processing (Frewen et al., 2020; Qin et al., 2020).

Finally, as this predictive model implies reciprocal influences between content of experience and priors as well as between the different priors themselves, a change in one prior will result in changes in other priors. This will ultimately also influence subsequent experiences. For example, any experience during which my intention is directed towards my body as a physical object (when I look at it in the mirror or when I think about its shape and size) would rely on — and at the same time influence — priors related to multisensorial inputs integration. Reversely, any experience engaging my sensorimotor body would influence priors related to — and thus subsequent experiences engaging — the intentional body as an object and the non-bodily self. During any experience, the nature of this experience (i.e., the intentional object, the subject current states, the context …) makes the central instance prioritize certain parameters for the generation of phenomenal content; but that does not prevent the whole set of top-down priors to be engaged. Such interdependence between priors at different levels allows identifying interaction between different dimensions of bodily experiences.

6. Neural implementation

Describing the neural correlates of this theorical model exhaustively would be challenging. Yet, as recent reviews highlighted, key networks of cerebral regions seem instrumental for different bodily self-experiences. Our model maps onto functional properties of and interaction between these networks.

Reviewing brain imaging, brain interference and lesion studies on different functions of somatosensation, de Haan and Dijkerman (2020) highlight key regions for contributing to body ownership and perception of somatosensory signals. More broadly, they proposed a model with five overlapping and interconnected networks that can be equated to different dimensions of bodily experience, namely haptic object recognition, body perception (i.e. perception of somatosensory signals), body ownership, action related sensory processing and affective body perception (i.e somatosensory information that have a social and affective meaning). The overlapping and multimodal nature of these networks could support interaction between dimensions of bodily experiences and the self. Specifically, the authors highlight a number of key nodes that are involved each in several networks: (i) the inferior parietal cortex, part of the "haptic object recognition", "body perception" and "body ownership" networks; (ii) the superior parietal cortex part of the same networks as well as "action related somatosensory processing" (i. e. all but the "affective body perception"); (iii) the ventral premotor cortex part of the "action-related" and "body ownership" networks and (iv) the anterior insula, part of the "body perception", "affective body perception" and "body ownership" networks, while the anterior cingulate cortex is assigned to the "affective body perception" and "haptic object recognition" networks. In addition, they place the somatosensory cortex (SII) and the ventral posterior lateral nucleus of the thalamus (i.e the main entry for signals from external receptors) in all five networks. Although de Haan and Dijkerman (2020)'s review is not quantitative, it concurs to a model where body ownership feeling would be subtended by parietal regions, the somatosensory cortex, the ventral premotor cortex, parts of the insula, thalamus, and cerebellum.

This model is in line with several brain imaging studies that investigated body ownership experience. These studies have used rubber-hand or full-body illusions contrasting conditions where multisensory stimulation is congruent and gives rise to a stronger percept of embodiment of the external body, to incongruent conditions with low ownership feeling over the external-body. The first neuroimaging study on the rubber hand illusion using functional magnetic resonance imaging (fMRI) found increased activity in premotor and intraparietal areas (Ehrsson, 2004). The first study using full-body illusion reported activation of the same regions (Petkova, Björnsdotter et al., 2011). Subsequent studies on the ownership illusion have been conducted that suggest the involvement of additional brain regions. Four metalanalyses of 16-19 of these studies (Grivaz et al., 2017; Nilsson and Kalckert, 2021; Salvato, Richter et al., 2020; Seghezzi et al., 2019) report convergent activity in parietal regions (intraparietal sulcus and/or inferior parietal lobule) and in the precentral cortex corresponding to premotor areas. Additional clusters are reported in the postcentral cortex, the insula (at a lower threshold) (Grivaz et al., 2017) and cerebellum, inferotemporal and fusiform cortice (Salvato, Richter et al., 2020). On their side, Park and Blanke (2019) reviewed work on neural bases of bodily experiences not restricted to body ownership but including also self-location feelings. They integrate notably studies that manipulate self-location through induction of out-of-body experiences (Guterstam et al., 2015; Ionta et al., 2011). They proposed that interoceptive and somatosensorial signals are combined to give rise to bodily self-consciousness. They put forward, as an underlying neural basis, a network that includes regions in precentral, intraparietal and insula as well as posterior cingulate cortex and temporo-parietal junction.

Some of these regions, supporting bodily self-consciousness have also been reported to be engaged during intentional explicit self-processing. Many studies used tasks where the subject must explicitly turn his intention towards himself, for example by answering questions like "Does the word 'honest' describe you?" or "Are you a student?". Using meta-analyses, with a large inclusion of studies of explicit self-referential experiences involving the "mental self", i.e. reflecting on personality traits, or the "physical self", i.e. reflecting on bodily physical features, Frewen et al. (2020) identified overlapping probabilistic convergent activity in the insula, temporo parietal junction, medial prefrontal cortex and inferior parietal cortex. This set of regions could therefore have a role in linking bodily self-consciousness and high-level mechanisms sustaining intentional self experiences. This is in line with Qin et al., (2020)' s three-level model linking "bodily, environmental and mental states in the self", which highlights the insula, temporo-parietal junction, rostral medial prefrontal cortex and precentral cortex, as common regions serving self/other distinction in different domains. Also, temporo-parietal junction and the rostral medial prefrontal cortex are part of the default mode network, which, as a whole, has been implicated in implicit self-related processing in general (Northoff, 2016). It would be interesting to explore further the relationship between the neural activity associated with implicit self-consciousness, on a one hand, and different dimensions of bodily experience, on the other hand. Interestingly, Tacikowski et al. (2017) reported that the rostral medial prefrontal cortex, together with the superior temporal gyri, hippocampus and retrospenial cortex, was sensitive to self-related semantic information but not object-related information, only when this information was consciously perceived and not when it was masked. In contrast, unconscious non-bodily self--processing, through visual masking, was associated with activity in the inferior temporal cortex. Some work needs thus to be done to understand the role of these regions for non-bodily self-processing and bodily self processing at the conscious and unconscious awareness level.

In summary, a number of brain areas are involved in different processes pertaining to bodily self-consciousness, exteroceptive and interoceptive perceptions , perception of the bodily and non-bodily intentional self. The central place of the sensorimotor cortex is consistent with its role in exteroception but also in experiences akin to estimating the size and shape of the body as an intentional object (Giurgola et al., 2019) and in predictive coding as modeled at cellular (Brecht, 2017) and whole-brain levels (Adams et al., 2013). Therefore, the sensorimotor cortex appears as a central element at the crossroad between different components of bodily experiences. This is concordant with the fact that, although not always explicitly discussed, in most definitions of bodily self-consciousness lies the idea that the sense of self is structured by our capabilities to control our movements and actions. The experience of being an embodied subject is indissociable of the experience of being an acting subject (Berthoz, 2000). Planning an action is constrained by the body serving as a support for action in the same way that the multisensory inputs are dependent on the action plan and on the executed movements. In fact, the intention of action alone modulates multisensory integration based on prediction mechanisms. Another important region is the cerebellum, which De Haan and Dijkerman attribute only to the "body ownership" and "action related" somatosensory processing networks (de Haan and Dijkerman, 2020). The cerebellum has been involved in forward and inverse internal models of action planning (Wolpert et al., 1998) but also in predictive coding in general (Sokolov et al., 2017). So, the cerebellum is certainly another hub involved in relating various bodily experiences. Fronto-parietal regions jointly with occipitotemporal regions are important for representing the body, own and other (Hodzic et al., 2009). They could be a substrate for storing priors about general shape and body size. It is noticeable that medial prefrontal and fronto parietal regions and insula, also participate in other people's perception (Grosbras et al., 2005), and thereby could be involved in integrating information from bodily self with information about the social aspects of the body. Different parts of the insula could be involved in linking the sense of bodily self to more general knowledge about the body and the social world. The ventral medial prefrontal cortex in contrast is more related to more abstract self-representations (Hu et al., 2016; Molnar-Szakacs and Uddin, 2013).

We listed different regions that are implicated in different networks. The functional connectivity patterns within and between these networks might support the relationships between the different levels composing the generative model we propose. The corresponding information is likely to be carried by specific rhythms in the brain (Bastos et al., 2015). In addition, it has been proposed that self-referential processing is related to temporal patterns of intrinsic brain activity, across different frequencies, operating on relatively long timescales (Kolvoort et al., 2020; Wolff et al., 2019). It would be interesting to investigate to what extent these spatio-temporal features of connectivity could relate to experiences of the body as an object or as a subject (Northoff and Stanghellini, 2016). Ultimately future research should establish more precisely how the flexible dynamic organization of the regions we outlined adapt as a function of experiences to support learning of weighting rules and updating of priors.

This view is obviously partial, eluding for instance the role of subcortical regions. The point is that existing brain imaging and neuropsychological data are in line with the view that the different dimensions of bodily experiences are supported by a specific set of delineated interconnected areas, whose dynamic functional organization allows for specific and varied bodily experiences underlying bodily self-consciousness.

7. Discussion

7.1. *Consistency with empirical studies originating from representationalist approaches*

The model presented above allows representing the multidirectional relationships between different dimensions of bodily experiences and the self. It allows integrating a wealth of empirical data showing that multisensory bottom-up and top-down processing shape the content of experience when we turn our intention towards our body as an object. The influence of peripheral somatosensory signals on the content of experience has been evidenced for example by Gandevia and Phegan (1999) who showed that, following peripheral nerve block or local anesthesia (or cutaneous stimulation), healthy subjects misestimate the size of the anesthetized (or stimulated) body part. Central mechanisms related to integration of bottom-up sensorimotor signals also influence the content of this experience. Giurgola et al. (2019) applied repetitive transcranial magnetic stimulation (rTMS) over the primary somatosensory cortex to interfere with the integration of sensorimotor inputs from the hand. They observed that participants overestimated the size of their own hand. Interoceptive signals also influence the phenomenal experience of the body. Sensitivity to interoceptive sensations, measured with questionnaires, correlates with the emotional component of body image (Duschek et al., 2015; Emanuelsen et al., 2015) or self-consciousness objectification (Ainley and Tsakiris, 2013). Salvato, Romano et al. (2020) showed that participants who tolerated negative bodily interoceptive signals better were less susceptible to malleability of the affective content of experience of the body as an object following exposition to extreme-sized bodies (thin or fat). These studies showed however only correlations between subjective interoceptive perception (i.e., what happens in the phenomenal consciousness of the subject) and phenomenal content of experiences implying the body as an object. The mechanisms by which objective interoceptive inputs influence how we experience our body as an object still needs to be investigated. Empirical evidence also supports the idea that the content of experiences can impact stored priors at unimodal as well as at more abstract levels, and thus influence subsequent experiences. For example, participants improve their interoceptive accuracy after being engaged in a task that forces them to focus on aspects of the body as an object ("focusing on their body image") (Filippetti and Tsakiris, 2017). The same result has been observed when directing the intention of the participants towards bodily or narrative aspects of self-consciousness (participants gazed respectively at a photograph of their own face or at self-consciousness-relevant words) (Ainley et al., 2013).

7.2. *Relationship between our model and other models and theories of bodily experiences and the self*

Other models relate the body and the self to general principles of perception. Qin et al. (2020) have proposed that the self relies on neural mechanisms that integrate three levels of information processing: interoceptive, exteroceptive and mental-self. Our approach differs from theirs in several aspects. First, we place at the center of our model the differentiation between the self as a subject and the self as an object (see Legrand's, 2007). On their side, Qin et al. (2020) aggregate findings from studies that have investigated the self as a subject (i.e. ownership illusions) and studies on the self as an object (i.e. paradigms implying a reflexive/introspective angle). They briefly allude to this distinction in the discussion of their manuscript and propose to anchor the self as a subject in exteroceptive-processing and mental-self-processing but not in interoceptive processing. We take another perspective and propose that the self as a subject is supported by interoceptive and exteroceptive multisensorial processing as well as mechanisms implicated in high-level cognitive functions. Secondly, our model places more emphasis on the interactions between the different levels organizing the generative model rather than considering a purely hierarchical organization. In particular we explicitly represent the bidirectional link between the perception of the external world and the combination of bottom-up multisensorial inputs and implicit self-related processing (as in G. Northoff's earlier claim (Northoff, 2016).

Other models focused on *self-referential processing,* defined as how we respond to stimuli that explicitly reference ourselves, i.e. the self as an object (Frewen et al., 2020; Hu et al., 2016; Sui and Humphreys, 2015, 2017). For example, Frewen et al. (2020) or Hu et al. (2016) distinguish physical and psychological self as object. They refer to tasks where the participant has to direct his intention towards his feeling or acting body and highlight differences and commonalities with tasks involving directing intention to non-bodily personal features. It has to be noted however, as we already pointed in the introduction, that "bodily self--consciousness" for them (which they equate to intentional "physical self"), differs from the concept of bodily self-consciousness operationalized in bodily illusion paradigms and phenomenology. Indeed, the latter presuppose pre-reflexive, non-intentional and implicit experience of the body. This difference in definition could create misunderstandings in future works on self-consciousness and bodily experiences.

Our model highlights that traditional representational theories are compatible with recent models that put forward multisensory integration and predictive processing; they "just need to be complexified" (Clark, 2008, 2013). 'Body image' and 'body schema' representations can be mapped into different parts of the model, as a function of the contexts in which these representations are used.

Also, Bayesian and predictive models allow to bring together representationalist approaches and phenomenological theories of bodily-self experiences. Bayesian models containing weighting rules and priors shaped by experience are compatible with Merleau-Ponty's definition of body schema *("a set of* sensorimotor laws built through experience that constrain the perceptual and motor experiences"). The rapprochement of phenomenology and cognitive sciences, two domains that had long been opposed in the study of the mind (Smith and Thomasson, 2005) (see Fig. 1), was advocated by Varela (1996; 1993)) and initiated a range of embodied and enactive approaches linking body and cognition. Our model goes well together with these approaches, as it depicts common processes underlying different bodily experiences, self consciousness and cognition. It enriches them by clarifying the dimensions of bodily experience embodied cognition approaches are referring to (Steiner, 2014).

Our framework also intersects with social psychology theories such as self-perception theory, which provides a psychological explanation of how people update their believes about themselves, and thus for example about their body appearance, as a function of their behaviour. Predictive processing complements this framework by linking it to neurophysiological mechanisms that support flexible multisensory integration.

7.3. Application to integrate existing findings on anorexia nervosa

Predictive models can account for the multidirectionality and multimodality of the relationship between different dimensions of bodily experiences and the non-bodily self. By bringing together different areas of research, this could help to better understand bodily experiences in atypical populations such as people with anorexia nervosa (AN). AN patients exhibit alterations in tactile (Keizer et al., 2011, 2012), haptic (Grunwald et al., 2001), proprioceptive and interoceptive perception of the body (rev in Gaudio et al., 2014). In addition, Campione et al. (2017) reported that motor representations – assessed via a hand laterality task, in which the subject has to mentally rotate her own hand (self--consciousness stimuli) or someone else's hands (other-stimuli) in order to provide a laterality judgement – are compromised. Besides, individuals with AN have been reported to experience a stronger rubber hand illusion (Eshkevari et al., 2012; Mussap and Salton, 2006). Possible explanations for these results through the lens of the model presented above could be that, in people suffering from AN, distorted inputs are not considered as not reliable by the central dynamic integrative instance and/or that the priors have a low precision and robustness (see Riva and Dakanalis, 2018). Recent studies, however, did not report a stronger full-body illusion in anorexic patients compared to healthy controls (Provenzano et al., 2019). This fuels debates about whether people with AN experience their body size and shape to be larger than they actually are. In fact, as presented above, the tasks used to evaluate the way people perceive their body size and shape are subject to much criticism. Manipulating body-ownership illusions may enlighten this debate. We think in particular of studies conducted in healthy participants that induced an ownership illusion over a body larger or thinner than the participant's body (Normand et al., 2011; Preston and Ehrsson, 2014, 2016; Rubo and Gamer, 2019; van der Hoort et al., 2011), and thereby questioned distortions of the pre-reflexive and non-intentional experience of the whole body size and shape.

One strength of our model is that it connects different approaches of the etiology of AN. Specifically, it allows a neurophysiological explanation of the "*feeling of strangeness of the body*" often reported in AN (Houssier, 2020; Viodé and Maïdi, 2020). In the same way as distorted integration of vestibular information impacts the feeling of first person perspective (Lopez and Elzière, 2018), one could hypothesize that distortion of multisensorial integration – especially interoceptive and somatosensorial inputs – would impact the feelings of agency and body ownership, and thereby create a feeling of strangeness. This model also supports a novel explanation of why AN patients often engage in intense physical activity. In addition to expanding energy consumption, high intensity practice could be a way for patients to increase the intensity of the inputs arising from the body and improve their capability to feel their body from the inside. Our model also offers clinical perspectives. If individuals with AN exhibit troubles at different levels, a successful therapy should rely on a multidimensional intervention. While therapeutic interventions could have an impact on high levels of the generative model (social and non-bodily-self levels), interventions implying the whole sensorimotor body – as massage, slow swimming, slow dance or slow exercise as yoga – would impact the lower levels (unimodal and multisensorial levels). At the opposite, clinical approaches targeting only one level, like when prohibiting any physical activity should be taken with caution.

7.4. Perspectives and limitations

Our model brings together separate theorical and empirical accounts related to the bodily and non-bodily self. Despite the questions it addresses having a longstanding record in philosophy and psychology, there is still a lot to understand from a neuroscientific point of view, especially when it comes to integrating higher-level factors. Furthermore, isolating neuronal activity carrying out prediction or prediction errors remains a challenge, which has been tackled, with mitigated success, with respect to basic visual perception (Walsh et al., 2020) but bears an additional level of complexity when it comes to account for the whole body.

Some parts of our model rely on findings that should be consolidated.

For example, to our knowledge, results showing a link between body ownership illusion susceptibility and interindividual differences in externally oriented cognition (David et al., 2014) are still few. More studies are thus needed to confirm this link. Also findings of decreased temperature during the rubber hand illusion, which could be explained by active inference for sampling interoceptive inputs, have been questioned and should be revisited (de Haan et al., 2017). More broadly, our model is built by combining results of studies investigating each only one aspect of bodily self-consciousness (for example focusing on body ownership illusion and high-level cognitive function only). It would be useful to design studies to identify the prevalence of each source of information and the interaction between these sources as a function of context. This could be achieved by combining bodily self-consciousness, self-consciousness and/or self-referential processing paradigms with a fine characterization of the subject psychological and physiological traits. In this way, one could question which factors have an effect on which task, and thus strengthen the empirical evidence for different parts of the model.

The mutual influence between social, cultural and educative factors on the one hand and bodily self-consciousness and multisensory integration (McCabe et al., 2006; Maister et al., 2015) on the other hand, could be addressed by combining, in the same study, tasks involving the neurophysiological dimension of the body and/or illusion paradigms, with tasks involving emotional or social dimensions of bodily experiences and/or the self - like in emotion regulation tasks (Christoff et al., 2011) - as well as perception of the external world – like self-other distinction tasks (Keromnes et al., 2019). Coupling body ownership illusion and self-related processing tasks would also enlighten the links between bodily self consciousness and self-consciousness, at the subjective and neural level.

To qualify how bottom-up internal sensory inputs- that is interoceptive, proprioceptive, and vestibular signals — affect subjective experience and how a person experiences the self and body as intentional objects, researchers have used questionnaires (Ainley and Tsakiris, 2013; Duschek et al., 2015; Emanuelsen et al., 2015), thus focusing only on subjective interoception, and interindividual variance. To confirm this link, one could study for example how experience of the body as an object is related to neurophysiological interoceptive inputs integration by recording brain responses to heartbeat as done in some studies cited above (Babo-Rebelo et al., 2016; Babo-Rebelo et al., 2019, Park, 2016). Also, it would be interesting to test whether a manipulation of sensory inputs integration abilities has an effect on the way a subject experiences herself objectively. It could be done for example by investigating if a period of training aiming to enhance multisensorial integration accuracy influences self-related processing.

Studying various dimensions of bodily experiences in specific groups could also be informative. For example, the literature in movement sciences, psychiatry and clinical psychology highlights adolescence as a critical period for experiences engaging the emotional dimension of the body (Laporta-Herrero et al., 2020), for neurophysiological signals (Assaiante et al., 2014; Cignetti et al., 2013) as well as for the non-bodily self-concept (Crone and Fuligni, 2020; Pfeifer and Peake, 2012) and for social cognition (Grosbras et al., 2018; Ross et al., 2012). This period is also crucial for the development of brain areas implicated in these experiences (Blakemore, 2012). To our knowledge, no study in cognitive neuroscience has focused on how bodily self-consciousness evolves in adolescence. This seems however of major importance given that many psychopathologies related to the bodily self and self-consciousness start in this period of life. The fact that participants with autism are markedly less susceptible to the rubber hand illusion (Cascio et al., 2012; Paton et al., 2012) and full body illusion (Mul et al., 2019) also opens the door for new hypotheses about specific predictive abilities in this population and for studies framed within this model.

Understanding more precisely the interaction between different dimensions of bodily experiences could also be leveraged in integrative medicine approaches, for example for chronic or phantom pain conditions or psychosomatic phenomena. Several recent empirical studies have reported a relationship between unexplained pain in the body and a disturbance in bodily self-experiences (Eccleston, 2018; Markey et al., 2020; Schwoebel, 2001; Senkowski and Heinz, 2016; see also review Di Lernia et al., 2016; Tsay et al., 2015). Influencing bodily self-experience may in turn modulate physiological mechanisms related to pain threshold as already proposed by Riva (2018).

Some issues should be noted. Firstly, we considered bodily self-consciousness as a whole, while it has been conceptually separated in four different feelings. The commonalities and differences between ownership, agency, first-person perspective and self-location should be addressed further in the framework of our model. Secondly, a strong premise, shared by the scientific community and on which we rely, is that we can experimentally study bodily self-consciousness, which is pre-reflexive. This can be done through bodily ownership illusions and asking the subject to explicitly report his subjective experience. This explicit report necessarily implies a time of reflection for the subject. Gallagher pointed however that any "reflection produces phenomena which are not necessarily contained within pre-reflexive experience" (Gallagher, 1986).

8. Conclusion

In summary, the relationship between the motor, multisensorial, affective, cognitive and social dimensions of bodily experiences is a central issue for many research fields such as clinical psychology, psychiatry, cognitive neuroscience, philosophy of mind and phenomenology. The classical dual representational model is limited in embracing the complexity of this issue as it does not address all the relationships between the different dimensions of bodily experience in a single model. This question ultimately concerns the central problem of the link between neurophysiological processes and subjective experience of being a self and is not restricted to the body. This paper advocates that, to relate the motor, multisensorial, and the subjective experience of the body, we need to broaden research on body representations. We therefore propose to merge phenomenological and predictive coding approaches to progress towards a richer understanding of the relationships between multiple dimensions of bodily experiences. This outlook emphasizes that there is no experience involving only the body as an intentional object, or only the body for acting and perceiving or only neurophysiological bodily inputs. Instead, the content of phenomenal consciousness can be traced in the balance between neurophysiological multisensory inputs and the brain activity related to unimodal inputs, the multisensorial integration, the body as an object in the external world, the non-bodily self, and the external world. Conversely, the content of experience influences stored generative priors of the external world, the self and the bodily self, and impact lower-level mechanisms (through active inference) as well as subsequent phenomenal content (through prediction updating). This approach has theorical implications for fundamental research and for pathologies such as anorexia nervosa and psychosomatic disorders.

The mechanisms that support the different ways in which we experience our body, their interactions, and their neural bases, are far from being fully understood. We hope that our model provides a foundation for more integrative and interdisciplinary research. In a broader perspective, this model participates to address the long-standing problem of mind-body relations.

Competing interests statement

The authors declare no competing interests.

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