Body schema and body image - pros and cons

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Reviews

Body schema and body image—Pros and cons

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ABSTRACT

There seems to be no dimension of bodily awareness that cannot be disrupted. To account for such variety, there is a growing consensus that there are at least two distinct types of body representation that can be impaired, the body schema and the body image. However, the definition of these notions is often unclear. The notion of body image has attracted most controversy because of its lack of unifying positive definition. The notion of body schema, onto which there seems to be a more widespread agreement, also covers a variety of sensorimotor representations. Here, I provide a conceptual analysis of the body schema contrasting it with the body image(s) as well as assess whether (i) the body schema can be specifically impaired, while other types of body representation are preserved; and (ii) the body schema obeys principles that are different from those that apply to other types of body representation.

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Until the end of the XIXth century, bodily awareness was conceived as a bundle of internal bodily sensations. In 1905 Bonnier first introduced the term “schema” to refer to their spatial organization. Since then, almost all neurologists have agreed on the existence of mental representations of the body, often called *body schema* or *body image* (or both at the same time). However, there has been a widespread confusion about the nature and the properties of these notions (Gallagher, 1986). And this is not surprising, given the variety of ways we have of relating to our bodies (e.g., through touch, vision, proprioception, motor behavior, semantic understanding, emotional affect, etc.) and the variety of disorders of bodily awareness (see Table 1).

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Table 1
Some disorders of bodily awareness.

Bodily disorders	Definition
Alice in Wonderland Syndrome	Distorted awareness of the size, mass, shape of the body or its position in space (including macro/microsomatognosia and OBE)
Allochiria (or dyschiria)	Mislocalization of sensory stimuli (tactile, visual, auditory) to the corresponding opposite half of the body or space
Allodynia	Pain due to a stimulus that does not normally produce pain
Anarchic hand sign	Unintended but purposeful and autonomous movements of the upper limb and intermanual conflict
Anorexia nervosa	Eating disorder characterized by self-starvation
Anosognosia	Lack of awareness of one's deficits like hemiplegia
Autoscopy	Experience of seeing one's body in extrapersonal space
Autoprosopagnosia	Inability to recognize one's own face
Autotopagnosia	Mislocalization of body parts and bodily sensations
Body form agnosia	Deficit of recognition of body parts
Body Integrity Identity Disorder (BIID)	Urge to be amputated of one's own perfectly healthy limb(s)
Body-specific aphasia	Loss of lexical knowledge of body parts
Bulimia nervosa	Eating disorder characterized by recurrent binge eating, followed by compensatory behavior.
Conversion disorder (hysteria)	Functional disorder with no organic cause
Cotard syndrome	Delusional belief that one is dead, does not exist, is putrefying or has lost one's blood or internal organs
Deafferentation	Loss of tactile and proprioceptive information
Depersonalization	Altered, detached or estranged subjective experience
Dysmorphophobia	Distorted perception of one's self-appearance
Fading limb	Lack of awareness of the presence and position of the limb if not seen
Finger agnosia	Inability to individuate and recognize the fingers
Gerstmann's syndrome	Finger agnosia, agraphia, acalculia and left-right confusion
Heautoscopy	Visual hallucination of a double of oneself at a distance
Heterotopagnosia	Designation of parts of the body of another person when asked to point towards one's own body
Hyperalgesia	Increased response to a stimulus that is normally painful
Hypochondrias	Excessive somatic concern
Ideomotor apraxia	Inability to execute or carry out skilled movements and gestures
Interoceptive agnosia	Loss of pain feeling
Macro/microsomatognosia	Distorted awareness of the size of the whole body or of body parts (bigger or smaller)
Mirror sign	Inability to recognize one's own image in the mirror
Misoplegia	Hatred towards one's own body parts
Motion sickness (or kinetosis)	Vestibular balance disorder
Motor neglect	Underutilisation of one side of the body
Numbsense	Tactile deficit with preserved tactually guided movements
Out of the body experience (OBE)	Visual awareness of one's own body from a location outside the physical body
Personal neglect	Lack of attention towards one's side of the body
Phantom limb	Awareness of an amputated limb
Pusher syndrome	Postural deviation towards the contralesional side
Prosopagnosia	Deficit of face recognition
Somatoparaphrenia (or asomatognosia or Alien Hand)	Denial of ownership of one's body part
Supernumerary limb	Awareness of non-existent limbs
Tactile extinction	Lack of awareness of tactile stimuli on the contralesional limb during simultaneous bilateral stimulation

One might therefore be tempted to conclude that one single body representation cannot suffice to account for such complexity. There needs to be more than one mental representation of the body. But how many? Two? Three? Four? Although there is a growing consensus that there are at least two distinct types of body representation, the body schema and the body image (Dijkerman & de Haan, 2007; Gallagher, 2005; Head & Holmes, 1911; Paillard, 1980), there is still little agreement beyond that, as we shall see here. Some may conclude that we would be better off without these notions:

> "We allow ourselves to speak of the body image and other such scheme or ghosts, which, I think, we would well be rid of by adopting a method of intellectual exorcism." Spicker, 1975, p. 182

It is one thing to get rid of the confusion in the literature; it is another thing to get rid of the notions of the body schema and the body image themselves with no further argument. Just because it is a "slippery issue", as it has been suggested (Holmes & Spence, 2005, p. 16), that does not mean that one should avoid it. Body representations are not ghosts. Every single morning, they allow us to comb our hair, to grasp our cup of tea, and to enjoy the warm feeling of the sun on our skin. And as soon as they are disturbed, we quickly realize that they play an important role in our life. So yes, we should adopt a method of intellectual exorcism, but only to clarify the conceptual landscape of the study of body representations. Here, I shall review the dominant models of body representation, namely, the neuropsychological taxonomies. I shall show the difficulties encountered by these models, both at the empirical level and at the conceptual level. I shall then conclude by proposing a more dynamic model based on Bayesian mechanisms of multimodal integration.

1. Taxonomies of body representation

Bodily disorders can be encountered in various contexts, both neurological (after brain lesion, peripheral lesion, migraine and epileptic seizure) and psychiatric. There seems to be no dimension of bodily awareness that cannot be disrupted (see Table 1). One of the main reasons one may want to postulate multiple types of body representation is to account for such variety.

How to organize the diversity of syndromes that differ on so many levels? For a long time, the syndromes were called "disturbances of the body schema" in the neurological literature and "disruptions of the body image" in the psychiatric literature (Denes, 1990). However, as noticed by Poeck and Orgass (1971, p. 255), "the only obvious common denominator was that they had something to do with the human body".

First, one may try to classify them along the lines of their clinical descriptions. Some bodily disorders result from *deficits*, like somatosensory loss in deafferentation. Others result from *distor-*

tions, like the feeling of expanding in macrosomatognosia. A further distinction can be done among patients, depending on the level at which they acknowledge the disorder. In some cases, patients have abnormal bodily experiences, but do not take their experiences at face value (e.g., 'as if' there were a limb). In other cases, patients have abnormal beliefs that are not grounded in abnormal bodily experiences (e.g., they mistake their index finger for their thumb). Finally, in other cases, patients have both abnormal experiences and abnormal beliefs (e.g., they feel, and believe, that it is not their own hand).

The neuropsychological principle of double dissociation can provide another way of classifying bodily disorders. A double dissociation is observed if a patient or group of patients is impaired on A, but not on B, and if another patient or group of patients is impaired on B, but not on A. If A and B are two body-related tasks, then there must be two independent processing systems of body information, which can be functionally dissociated by lesions. I shall focus here on two main taxonomies of body representation that are based on this principle, but it is worth noting that there are other taxonomies using different criteria (e.g., short-term versus long-term body representations, cf. O'Shaughnessy, 1980; my body versus your body, cf. Felician, Ceccaldi, Didic, Thinus-Blanc, & Poncet, 2003).

The dyadic taxonomy (Dijkerman & de Haan, 2007; Gallagher, 2005; Paillard, 1999; Rossetti, Rode, & Boisson, 1995): The dyadic taxonomy draws a distinction between the body schema and the body image. The body schema consists in sensorimotor representations of the body that guide actions. The body image groups all the other representations about the body that are not used for action, whether they are perceptual, conceptual or emotional (body percept, body concept and body affect, cf. Gallagher, 2005). Several dissociations have been proposed to ground the dyadic taxonomy, such as the double dissociation between deafferentation (disruption of body schema) and numbsense (disruption of body image) (Paillard, 1999).

The triadic taxonomy (Schwoebel & Coslett, 2005; Sirigu, Grafman, Bressler, & Sunderland, 1991): The triadic taxonomy retains the dyadic taxonomy's notion of body schema. That is, it maintains that there is a sensorimotor representation based on afferent and efferent information, but rejects the notion of body image because of its heterogeneity. Consequently, the body image is split up into two distinct body representations: the body structural description (or visuo-spatial body map) and the body semantics. At the visuo-spatial level, the body image provides a structural description of the relationships between body parts (i.e. their boundaries, their proximity and their position relative to each other). It is primarily based on vision, but also on somatic perception. At the semantic level, the body image is primarily conceptual and linguistic. It describes the functional purpose of body parts and the categorical relationship between them (e.g., wrist and ankles are both joints). The triadic taxonomy is grounded in the dissociation between apraxia (disruption of the body schema), autotopagnosia (disruption of the body structural description), and body-specific aphasia (disruption of the body semantics).

The notion of body image has attracted most attention (and controversy) because of its lack of unifying positive definition. The dynamics of the body image varies from short-term body percept to long-term body concepts. In addition, the body image can be applied both to one's own body and to someone else's body. And it seems to be both non-conceptual (body percept) and conceptual (body concept). Why are all these aspects part of one single category? It seems like the body image is just whatever is left over after we are done talking about the body schema. Consequently, the dyadic taxonomy is not fine-grained enough to account for the complexity of the body image. Yet, to what extent should one break down the body image into dissociable elements? There seems to be no end. So many dissociations are possible that three types of body representations may not even suffice.

In addition, what is a distinctive feature of the body schema by contrast with the body image(s) for one author may be irrelevant for another. Three main criteria have been used to draw the distinction between the different types of body representation: availability to consciousness (unconscious versus conscious); dynamics (short-term versus long-term); functional role (action versus perception). The weight of each criterion varies relative to the author. For instance, Head & Holmes favour availability and dynamics; Paillard exclusively highlights the importance of the functional role; Gallagher combines availability and functional role; Schwoebel & Coslett combine dynamics and functional role. It is no surprise therefore that the very same notion can be ascribed opposite properties by different authors. For instance, according to Cole and Paillard (1995), it is the body image that is holistic, whereas according to Gallagher (1995), it is the body schema.

It is more interesting to highlight what the taxonomies have in common, than to analyze each view in its differences with the others or to indefinitely try to figure out the exact number of body representations. Before fighting over the dead corpse of the body image, one should first investigate in more detail the (seemingly more robust) notion of a body schema. Despite their various disagreements, both the dyadic and triadic taxonomies seem indeed to agree on the existence of something called a body schema, distinct from something else, whatever that something else is called (body image, body structural description, visuo-spatial body map, body semantics, etc.). Furthermore, they both agree on the definition of the body schema as a sensorimotor representation of the body, highlighting a special relationship between the body schema and action. No successful action is possible without a representation of one's bodily parameters such as the size and the strength of one's limbs. It is thus highly plausible from an evolutionary perspective that body information processing evolved first to be used for action, and if one wants to study body representations, one should start with those that are action-oriented.

2. The Perception/Action model of body representations

There is one aspect on which almost all taxonomies seem to agree, namely, the importance of functional roles in differentiating various types of body representation, and especially the role of guiding action for the body schema (Gallagher, 2005; Paillard, 1999; Schwoebel & Coslett, 2005; Sirigu et al., 1991). This would seem to track the well-founded Perception–Action functional distinction, which has been shown first in vision (Milner & Goodale, 1995), but also later in audition (Belin & Zatorre, 2000), touch and proprioception (Dijkerman & de Haan, 2007).

Contrary to common sense and much philosophy of perception, human vision is *not* a unitary psychological activity, whose single purpose is to yield a unified conscious picture of the visible features of the world. As shown by a variety of empirical evidence, one and the same visual stimulus can be processed differently according to the task one is engaged in. Ungeleider and Mishkin (1982) first distinguished the *What*-system in the ventral stream dedicated to object recognition and the *Where*-system in the dorsal stream dedicated to object localization. Later, Goodale and Milner (1992) distinguished the *What*-system in the ventral stream and the *How*-system in the dorsal stream dedicated to visually guided actions. They ground their distinction on a double dissociation between two syndromes: optic ataxic patients who are able to make visual judgments, but unable to reach and grasp objects, and visual form agnosic patients who are unable to make visual judgments, but able to reach and grasp objects. Further evidence for the dual model of vision has been provided by studies on visual illusions in healthy participants, such as the Müller–Lyer illusion, the Ponzo illusion, the Titchener illusion or the hollow face illusion. For example, in the hollow face illusion, participants perceive a 3D concave (or hollow) mask as a convex (or protruding) face. If asked to quickly flick a target magnet off the face, they directed their finger movements to the actual or veridical location of the target rather than the apparent location of it, which was 8 in. away (Kroliczak, Heard, Goodale, & Gregory, 2006).

Paillard was strongly influenced by the Perception–Action model of vision and applied it to the analysis of body representations. Following Ungerleider and Mishkin, he first suggested distinguishing "the identified body" (*le corps identifié*) and "the situated body" (*le corps situé*) (Paillard, 1980). He then refined his model and made a distinction between 'knowing where' and 'knowing how to get there' (Paillard, 1991). In other words, the body image is dedicated to perceptual identification and recognition (e.g., body part judgments) and the body schema is dedicated to action (e.g., information about the body necessary to move such as posture, limb size, and strength) (Dijkerman & de Haan, 2007; Paillard, 1999).

It should be noted, however, that the Perception–Action distinction has been criticized both on empirical and theoretical grounds. It has been shown that in some circumstances, ataxic patients can use visual information to guide their movements and that action can be sensitive to certain types of visual illusions (for review, see Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006). However, what is challenged is not the hypothesis that there are two pathways, one of which is dedicated to action. What is challenged is the hypothesis that the two pathways work in isolation without interacting. As we shall see, the same is true of body representations. A second line of counter-argument may come from the enactive approach, which rejects the computational dichotomy between perception and action (Hurley, 1998; Noë, 2004; O'Regan & Noë, 2001). On this view, perceptual experiences constitutively depend on sensorimotor expectations. Hence, perceptual experiences are said to be inseparable from the perceiver's bodily activities. If this is true, there should be no reason to defend the body schema/body image distinction, and no way to dissociate them (for a full discussion of the enactive approach of bodily experiences, see de Vignemont, submitted for publication).

Therefore, the debate is whether we use a specific type of body representation to program and guide actions, which is distinct from the one used in perception. Everybody agrees that we use bodily information in various contexts and for different purposes, including action guidance. But does that mean that each purpose requires its own purpose-specific body representation? Does action make a difference for the way the brain represents the body? In other words, one may agree that body representations can play different roles, without accepting that there are different *types* of body representation. A purely functional distinction between body representations fails to logically exclude a single-process model, which would be more in line with the enactive approach. One has to disentangle two possibilities: one and the same representation used for different functions or different representations specific to each function. In order to argue for the latter hypothesis, one needs to show that: (i) action-oriented body representations can be specifically impaired, while other types of body representation are preserved; and (ii) action-oriented body representations obey principles that are different from those that apply to non-action-oriented body representations. That shall be my agenda for the remainder of the paper. But beforehand, I would like to explore in more detail the notion of body schema defined as a set of action-oriented body representations.

Let me start with the special case of reflective actions where one's body is represented both as the goal of the action and as the effector of the action (e.g., scratching a body part). It is often unclear in the definition of the body schema whether it represents both poles, and we shall see that it is especially unclear in some reflective actions like pointing to body parts. The body as a goal does not seem to differ much from any other non-bodily goals. I can reach for my head or I can reach for the book, and it does not seem right to say that the body schema represents the book. Yet, when the action is body-directed, there must be a sensorimotor representation of the body as the goal. When I reach for the book, my movement is guided by a visuo-motor representation of the book that recruits the dorsal visual system. Similarly, it makes sense to assume that when I reach for my head to scratch it, my movement is guided by a proprioceptive-motor representation of the head that recruits the body schema. A more interesting question, I think, is whether it is the same type of body schema that represents both the bodily effector and the bodily goal. In other words, is it possible for patients to be unable to reach for one body part, and yet be able to use this body part to perform actions? Unfortunately, the two aspects are rarely explicitly compared, but they seem to be dissociated in patients with numbsense for instance (Paillard, Michel, & Stelmach, 1983), as we shall see later. This leads me to the following definition of action-oriented body representations:

> *A body representation is action-oriented if and only if it carries information about the bodily effector (and the bodily goal in reflective actions) that is used to guide bodily movements.*

The question is then to determine what bodily information is required by action and how it is represented. I shall argue that the Perception–Action distinction is orthogonal to the distinction between short-term and long-term body representations, and between unconscious and conscious body representations.

The variety of dynamics and plasticity of body representations is a recurrent question in the literature. It has even been used as a key criterion to individuate distinct types of body representations (Carruthers, 2008; Merleau-Ponty, 1945; O'Shaughnessy, 1980; but also Head & Holmes, 1911; Schwoebel & Coslett, 2005). On the one hand, there would be short-term on-line body representations (or 'actual body' cf. Merleau-Ponty), which include the representations of the body posture at time t and which are constantly updated. On the other hand, there would be long-term off-line body representations (or 'habitual body' cf. Merleau-Ponty), which represent the long-term bodily properties such as the spatial organization of the body parts and their respective size and which are relatively stable.

Say we all agree that if there is something like a body schema, then it is action-oriented. Now, such a basic statement does not imply that the body schema is a short-term body representation, as it seems to be assumed by the triadic taxonomy for instance. Short-term representations are by definition representations with a very short life-scale. It is built up at time t, stored in working memory, and erased at time $t+1$ by the next one. And true, to move one's arm one needs to know its position at time t, and this information is no longer true at $t+1$. Yet, to move one's arm, one also needs to know its size, which has not changed for the last 10 years. For example, to switch on the light, you need to know the length of your arm in order to determine how far you should stretch your arm. You also need to know what types of movement your arm affords. Hence, action recruits both short-term and long-term bodily information. It is too costly to compute the size of body parts each time one thinks of moving. Rather, one may suggest that the body schema includes not only short-term body representations, but also long-term body representations.

Now, the question of consciousness is slightly more complex, and more controversial. In the case of vision, the functional distinction Perception–Action is tightly linked to the contrast conscious–unconscious. Milner and Goodale (2008) assume a restrictive link between visual awareness and vision-for-perception at the expense of vision-for-action. According to them, visuo-motor representations are not accessible to consciousness. That does not mean that one cannot be conscious of actions, but one has no access to the visuo-motor representations that guide the actions. On this view, the dorsal pathway is, in Pisella et al.'s (2000) terms, an "automatic pilot". On this view, agnosic patients would have no conscious experience of the properties of stimuli that they can accurately grasp. However, this view is disputed in the visual system literature and there is no empirical evidence in favour of it. True, agnosic patients do not report the accurate length of the object they can grasp. But that does not show that they are not aware of the length of the object. It is not because you cannot report it that you are not aware of it (Block, 2007; Lamme, 2003; Simons & Rensink, 2005). It is one thing to say that visuo-motor representations do not *require* consciousness, and it is another thing to say that they can never *be* conscious. As far as the evidence goes, only the former claim can be made for visually guided actions (Jacob & de Vignemont, in press; Wallhagen, 2007).

The same debate takes place for body representations. Head and Holmes (1911) claimed that body schemata are unconscious, while the body image is conscious. Similarly, according to Gallagher (2005), the body schema operates automatically at the subpersonal level and can never become conscious as such. One does not pay attention to one's limbs in movement, but to the world. But a lack of attention is one thing and a lack of awareness is another. One may indeed suggest that while acting, one is aware of one's body, although the body stays in the background, or the margin, of consciousness: "There is no moment in our conscious life when we are completely unaware of our bodily posture, of the fact that we are walking, standing, sitting, lying down." (Gurwitsch, 1985, p. 31).

Even without claiming that the body schema is all the time conscious, one may at least argue that it can be conscious in some circumstances, like in motor imagery (Schwoebel & Coslett, 2005). In motor imagery, one imagines one's body performing movements. It is now well documented that motor imagery shares many properties with physical actions at the physiological level (muscle activity), at the kinematic level (similar physical constraints and laws) and at the neural level (shared patterns of brain activation) (Jeannerod, 1997). As such, motor imagery constitutes a good task to assess the integrity of the body schema (Schwoebel & Boronat, 2002; Schwoebel & Coslett, 2005). What is interesting is that motor imagery can be conscious or not. For instance, in hand laterality judgments, participants imagine their own hand rotating so that it matches the visually presented hand (Parsons, 1987). Most of the time, mental rotation remains implicit, although participants can perform it explicitly and consciously without modifying their performance (de Vignemont et al., 2006). Another task to assess the body schema used by Schwoebel and Coslett (2005) is to explicitly ask patients to imagine performing actions. Again, the patients are consciously performing the action in their head. They have a conscious access to the mental representation of the body in action, namely, to the body schema. The body schema is then conscious. That does not mean that the computations involved in the construction of the body schema (e.g., multisensory integration) are available to consciousness, but the output, namely, the representation of the body in action can be conscious in some rare circumstances like motor imagery. Consequently, the availability to consciousness is not a criterion to differentiate the body schema and the body image.

More important as a defining feature of the body schema is its role in the motor hierarchy. The body schema is exploited by the motor system at different stages. In the computational framework, the motor system uses two types of internal models: the inverse model and the forward model (Wolpert, Ghahramani, & Flanagan, 2001). They both involve the body schema. The inverse model has the role of computing the motor commands needed to achieve the desired state given the agent's current body state. The inverse model is thus fed by the *initial body schema*, including long-term information like the size of the limbs, and short-term information like the joint angles and the hand position. In parallel, the motor system anticipates the sensorimotor consequences of the movement through the forward model. The forward model predicts what an action will be like given the specific body that executes the motor commands. It results in the *predicted body schema*, which carries information only about the bodily parameters that will be altered by the movement like the hand position. It is involved in motor imagery and allows anticipatory control of movements. Finally, there is the actual sensory feedback resulting from the execution of the action that provides the *updated body schema*, which again carries information only about the bodily parameters that have been altered. Consequently, both the predicted body schema and the updated body schema are dynamic short-term body representations, whereas only the initial body schema includes both short-term and long-term body representations. However, it is worth noting that during childhood, the child may learn that his arm is longer than before for instance by overreaching the jam pot. If so, the discrepancy between the expected arm size and the actual arm size leads to accordingly modify the initial body schema.

If indeed the body schema has to explain action program and guidance, then this is how it should be defined. But does one need a specific type of body representation to do that, one that would be different from the one used in perceptual reports about the body? I have provided here a theoretical definition of the body schema. It is time now to determine whether there is any psychological reality behind. Let us see whether there is empirical evidence in favour of the distinction between action-oriented body representations and the other types of body representation. In order to do so, we shall have to first determine what tools we have to specifically assess the body schema by contrast with the body image(s).

3. Pointing to what?

Very few tests have been developed to assess body representations. The task is made more difficult by the variety of aspects of body representation that can be evaluated. One may be interested in the shape and size of the body, in the position of body parts, or in the localization of bodily sensations. Each feature requires its own measure. For instance, the experimenter can appeal to visual matching with body templates for body size, to motor matching with the contralateral side for the posture, and to pointing to body parts for the localization of sensations. If one wants furthermore to dissociate between different types of body representation, then one needs specific tools to assess each type. The battery of tests that has been suggested to assess the body schema versus the body image(s) is actually limited, as shown in Table 2.

One task that has come back again and again since Head and Holmes (1911) is that of asking participants to point to a body part that has been either touched, or named, or visually shown on a picture. Although it is widely used, especially in neuropsychology, it is not clear what the pointing task is supposed to assess. On the one hand, it is taken as a measure of the body schema. As such, it is said to be impaired in deafferentation, but not in numbsense (Dijkerman & de Haan, 2007; Gallagher & Cole, 1995; Paillard, 1999; Rossetti et al., 1995). On the other hand, it is taken as a measure of the body image. As such, it is said to be impaired in autotopagnosia, but not in apraxia (Schwoebel & Coslett, 2005; Sirigu et al., 1991). In addition, sometimes it is a measure of both the visuo-spatial and the semantic components (Sirigu et al., 1991); sometimes it is a measure of the visuo-spatial body image only (Schwoebel & Coslett, 2005). Finally, it has been recently argued that it is not a measure of body representation at all, but rather a measure of non-verbal communication (Cleret de Langavant, Trinkler, Cesaro, & Bachoud-Lévi, 2009). This latter view, however, is supported by evidence on pointing to another individual's body parts. As the situation is

Table 2
Assessing the distinct types of body representation.

	Body schema	**Body image(s)**	
	Sensorimotor	*Visuo-spatial*	*Semantic*
Paillard (1999) Anema et al. (2009)	Pointing to one's body part	Naming one's body part Pointing to a pictured body part	
Semenza and Goodglass (1985) Sirigu et al. (1991)		Pointing to one's body part *Contiguous errors*	Pointing to one's body part *Functional errors*
Schwoebel and Coslett (2005)	Motor imagery	Pointing to one's body part and to a pictured body	Matching body parts to functions and body-related objects

already complex enough without adding someone else's body, I shall focus on pointing to one's own body parts. So, what do pointing errors mean? A disruption of the body schema or a disruption of the body image(s)?

The reply is that it can reflect both types of disorders. There are indeed two possible uses of most intentional hand movements. Most of the time, they are mere actions, performed for instance because one wants to do something with a specific object. When I scale the distance between thumb and index finger, it is because I want to grasp the object in front of me. However, in the experimental context, manual responses can also be used to give a perceptual report. For instance, I can scale the distance between thumb and index finger in order to report the size of the seen object. Interestingly, the underlying processes are very different, and patients with visual apperceptive agnosia are impaired in one, and not in the other (Milner & Goodale, 1995). Consequently, it is a mistake to assume that every manual response is action-oriented. And it is possible to dissociate the two uses of the same manual response, like in vision (Milner & Goodale, 1995), and like in touch (Anema et al., 2009).

The duality of use is especially true in the case of pointing response. The fact is that pointing is an unusual action. It is a communicative act that makes sense only in a social context. It is used to attract an observer's attention to a target and to indicate it. The function of the pointing gesture can be either declarative (e.g., infants point to share attention and interest) or imperative (e.g., infants point when they want the observer to bring the target). Pointing to body parts (rather than pointing to objects) is even more special. Pointing to body parts reaches an adult level only between 4 and 5 years of age (Poeck & Orgass, 1964), whereas most body-directed actions develop earlier. It involves representing the body both as the goal of the action and as the effector of the action. Surprisingly, however, what is measured in most studies is only the ability to localize the bodily goal, and very rarely the ability to make fast pointing movements, whether they are directed towards the body or not. The problem is that if you do not compare the two, then you cannot determine whether the participants have disturbed representation of the body as the goal or of the body as the effector.

Pointing gestures have thus an informative value, especially in clinical situations where the patients have to *indicate* the body part to the examiner. Here, it seems that pointing is more often used for perceptual report than for action. This is clearly the case for instance when patients are asked to point where they have been touched on a pictorial map of their hand (Anema et al., 2009). This is also the case in studies of autotopagnosia where patients are said to make errors if they point on their own body to the wrong body part (e.g., arm rather than hand), but not if they point to the wrong tactile locus in the correct body part (e.g., on the left side of the palm rather than on its right) (e.g., Sirigu et al., 1991). I suggest that in these studies, the patients are asked to give categorical judgments via a *manual report*. By contrast, when patients are asked to point on their own hand where exactly they have been touched, it is the precise spatial location within the hand that is measured (Anema et al., 2009). Similarly, in studies with deafferented and numbsense patients, the errors are spatial errors, rather than categorical errors (Paillard et al., 1983; Rossetti et al., 1995). It is the exact location on the palm that is required. This difference between the two types of studies may explain the two distinct interpretations of the pointing task. Categorical errors on one's hand would reveal a body image(s) deficit, whereas spatial errors on one's hand would reveal a body schema deficit.

A further and crucial difference between the studies is the availability of visual feedback. In some studies, patients see their body (Schwoebel & Coslett, 2005); in others, they are blindfolded (Paillard et al., 1983; Rossetti et al., 1995). Because in the former case, pointing movements are visually guided, they cannot be considered as ballistic. Ideally, a truly ballistic movement should be entirely accounted for by commands existing before its initiation executed without visual feedback (Jeannerod, 1997). When patients are not blindfolded, they can use on-line visual information about their body to help them and do not exclusively rely on an internalized body representation. They also have more time to perform the movement. Interestingly, it was shown that patients with visual deficit in dorsal stream are still able to make fairly accurate pointing movements after being instructed to slow down (Kroliczak et al., 2006; Rossetti et al., 2005).

Consequently, I would like to suggest that there is no contradiction between the two opposite interpretations of pointing errors either in terms of a body schema deficit or in terms of a body image deficit. Depending on the target (e.g., one's hand versus a hand map), on the type of errors measured (e.g., spatial versus categorical) and on the type of movements performed (e.g., slow visually guided informative gesture or fast ballistic movement), pointing might recruit different types of body representations. Nonetheless, it does not seem ideal to use an action to test non-action related body representations such as the body image(s). Nor is it certain that one never recruits the body image(s) when performing even fast ballistic pointing movements. Indeed, if one analyses what is really required by pointing, one soon realizes that pointing always taps both types of body representations: sensorimotor and visuo-spatial (and sometimes semantic as well). In order to point to where you have been touched with your right hand, there are several tasks that the brain needs to perform: (i) localization of the effector (e.g., where is my right hand?); (ii) identification of the target body part (e.g., what has been touched? the leg?); (iii) localization of the target body part (e.g., where is my leg relative to my hand?); (iv) localization of the stimulus site within the body part (e.g., where on my leg have I been touched?). Of course, none of these questions is raised consciously. But this does not show that one does not implicitly use body representations to answer them, and most probably these body representations have different spatial frames of reference, and are of different types.

To clearly dissociate the body schema and the body image(s), one would ideally need an experimental measure that is both exclusive (i.e. specific to one kind of body representation only) and exhaustive (i.e. representative of the whole body representation, and not only of part of it). However, the few methods that are used like the pointing task are neither exclusive nor exhaustive. Part of the answer might be to use reaching and grasping movements for testing impairments of the body schema rather than pointing movements (see Merleau-Ponty (1945) for an early account of the difference; see also Cleret de Langavant et al., 2009 for a dissociation between pointing and grasping in patients with heterotopagnosia). Typically, one reaches a body part to do something on it (e.g., to put a hat on, to scratch a mosquito bite, etc.), such movements are (most of the time) a mere step in a series of actions performed towards the body part. As such, reaching and grasping movements are more directly linked to the body schema. We shall see now how the lack of proper tools affects the interpretations of bodily disorders.

4. Neuropsychological dissociations

Most of the literature on body representation heavily relies on neuropsychological dissociations. However, a first thing one should note is that the neuropsychological dissociations exploited by current theories that posit multiple body representations are just a few among a long list of possible dissociations. Their taxonomies assume the existence of two or three types of body representation only, whereas they have to explain more than thirty kinds of bodily disorders, which are not easily classified, or at least not along the dyadic or triadic taxonomy. One may argue that the impairment of one and the same type of body representation can lead to different syndromes. However, if a putative disruption of the body image can lead to phenomena as diverse as Cotard syndrome (i.e. you believe your body is dead and rotting) and finger agnosia (i.e. you cannot name your fingers), then there is a risk of making the concept of a body image empty of meaning and explanatory power. There is an alternative that consists in assuming that each bodily disorder involves the breakdown of a different type of body representation. However, there are so many bodily disorders, and therefore so many possible dissociations, that one would end up with an almost infinite list of body representations. Pushed to its limits, the dissociative principle would no longer make sense.

One might agree that the neuropsychological taxonomies fail to provide an exhaustive account of all bodily disorders and still hold that the limited account is plausible. For it does not follow that the account provided of the limited number of pathologies directly targeted is false. One may further argue that those disorders are actually the clearest cases, and as such, offer a good grasp of what can be impaired in bodily disorders in general. The problem with this line of reasoning is that even those limited cases are not so clear, as shown by the completely opposite ways they are explained (see Table 3). Here, I shall highlight the complexity of most syndromes, such complexity often resulting from simultaneous deficits of the body schema and the body image(s). I shall conclude with a double dissociation that seems to be the most promising in the perspective of dissociating the body schema and the body image(s).

4.1. *Peripheral deafferentation: the "missing body schema" (Gallagher, 2005)?*

Following very rare acute sensory neuropathy, some patients become deafferented below the neck, i.e., they have no proprioceptive function and no sense of touch. Their motor system is spared and they are capable of movements. In addition, they experience hot, cold, and pain and retain their vestibular sense of balance. Yet, they have no inner sense of bodily posture. If they close their eyes, they do not know where their limbs are. Consequently, they have to learn to exploit visual information in order to know where their limbs are so that they can guide their movements. According to Gallagher and Cole (1995), major parts of their body schema are "missing", and compensated by a reflexive use of their body image.

But in what sense is the body schema defective? After all, they can move. You may not even be able to notice that there is anything abnormal when you meet them. As noticed by Travieso, Pilar, and Gomila (2007, p. 223): "What we think the results show is that G.L. [a deafferented patient] was simply poor at pointing without vision: she was equally good at pointing with vision towards her hand or towards a picture. Her problem was not with action itself, but with the use of haptic information alone (without vision)."

It does not make more sense to claim that deafferented patients have a deficit of body schema than to claim that blind people have a deficit of body schema. In the latter case, they rely on proprioception instead of vision. In the former case, they rely on vision instead of proprioception. The body schema (*qua* sensorimotor representation) is there, although based on different weighting of information. Whereas proprioception may normally play an important role, it has been taken over by vision in deafferented patients.

One may reply that their actions are not normal because they require reflexive monitoring of their movements. This might have been true at the beginning when the patients had to learn how to visually guide their movements. Similarly, you have to pay attention at the beginning when you learn to drive a car. But after a while, you drive without consciously monitoring the visual information that you receive on the other cars, the road, etc. Deafferented patients are like the automatic drivers. Their actions have become automatic routines that do not prevent them of simultaneously doing other activities like talking. This is not to say that their body schema has not changed. It has, giving more weight to vision. But it is not "missing".

4.2. *Apraxia: conceptual or sensorimotor deficit?*

A better candidate for a deficit of body schema may be apraxia (Buxbaum, Giovannetti, & Libon, 2000; Schwoebel & Coslett, 2005).

Table 3
Neuropsychological dissociations between multiple body representations.

<table>
<tr><th>Body schema</th><th colspan="2">Body image(s)</th></tr>
<tr><td>Sensorimotor</td><td>Visuo-spatial</td><td>Semantic</td></tr>
<tr><td>Deafferentation (Paillard, 1999; Gallagher, 2005)</td><td colspan="2">Numbsense (Paillard, 1999)</td></tr>
<tr><td>Personal neglect (Coslett, 1998)</td><td colspan="2">Personal neglect (Gallagher, 2005)</td></tr>
<tr><td>Apraxia (Buxbaum et al., 2000; Schwoebel & Coslett, 2005)</td><td colspan="2">Apraxia (Goldenberg, 1995)</td></tr>
<tr><td></td><td>Autotopagnosia (Sirigu et al., 1991; Schwoebel & Coslett, 2005)</td><td>Autotopagnosia (Sirigu et al., 1991)
Body-specific aphasia (Schwoebel & Coslett, 2005)</td></tr>
</table>

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It is generally defined as a disorder of skilled movements that cannot be explained by peripheral deficits (e.g., motor weakness, deafferentation, etc.). However, there may be as much as 29 different kinds of apraxia (for a full review, see Petreska, Adriani, Blanke, & Billard, 2007). They can be lesion-specific, modality-specific, task-specific, and effector-specific. They can be grouped into two main types. Ideational apraxia results from disturbance in the conceptual organization of actions. Ideomotor apraxia is considered to be a disorder of the production of sensorimotor programs. I shall focus on this latter type.

Most theoretical models explain ideomotor apraxia in terms of central motor deficits. There is, however, some evidence in favour of a bodily deficit. In clinical examination, it is often reported that patients with ideomotor apraxia mislocate the goal of their reflective actions (e.g., brushing chin rather than teeth). These patients demonstrate even greater deficits in locating the hand that will carry the action (Haaland, Harrington, & Knight, 1999). In addition, they have difficulties in imitating meaningful and meaningless gestures (Buxbaum et al., 2000; Goldenberg, 1995). Both types of imitation require the matching of someone else's body onto one's own body ("the body correspondence problem" Goldenberg, 1995). Meaningless gestures are of particular interest because they rely exclusively on the encoding of the bodily attributes of the movements (i.e. encoding the position of one's own body, abstracting the target position from individual differences, and matching one's position onto the other's position). There is no stored gesture information to confer a processing advantage in on-line meaningless imitation.

But at what stage are apraxic patients impaired? At the stage of the evaluation of the position their own body? At the stage of the evaluation of the target bodily configuration? And/or at the stage of the ability to map their own body with the target body? And what type(s) of body representation is impaired? The sensorimotor level or the conceptual level? According to Goldenberg (1995), ideomotor apraxia is due to a deficit of the general conceptual knowledge of the human body, which sounds like a body image. By contrast, Buxbaum et al. (2000) argue that ideomotor apraxia results from a deficit of the body schema.

It is especially hard to settle the debate as the experimental results are sometimes contradictory. First, it was found that apraxic patients are impaired on aiming movements without visual feedback (Haaland et al., 1999; Ietswaart, Carey, & Della Sala, 2006). Furthermore, they are impaired in some motor imagery tasks (i.e. mental rotation and imagining movements, cf. Buxbaum et al., 2000; Sirigu et al., 1996). However, they are not impaired in all motor imagery tasks (i.e. reporting the side on which the little finger appears from the patient's perspective when asked to imagine her hand in a particular position, cf. Sirigu et al., 1996). And spontaneous behavior is said to be relatively preserved in apraxia, although clumsy or awkward. In addition, Goldenberg (1995) found that apraxic patients have difficulties not only in imitating postures with their own body, but also in matching the position of the body parts of a life-sized manikin with the target bodily posture. This deficit seems to go beyond the consequences of an impairment of the body schema. Goldenberg argues that imitation requires abstracting from differences in spatial positions as well as from differences in the size and shape of the bodies. Consequently, it seems to rely upon general knowledge of the body, which applies also to manikins. We are far from the primary sensorimotor body schema guiding one's own movements.

To conclude, there are convincing hints that a disruption of the body schema contributes to ideomotor apraxia, but most probably it is only partial. It certainly does not exclude the possibility of a concomitant disorder of the body image.

4.3. Personal neglect: lack of attention towards the body image or the body schema?

The situation is even less clear for personal neglect. Personal neglect is clinically defined by a lack of exploration of half of the body contralateral to the damaged hemisphere. Yet, neglect patients do not complain about the missing half of their body. They feel as they always felt, as if their body were complete. Again, there are contradictory interpretations of this bodily disorder. It is conceived either as a deficit of the body image with a preserved body schema (Gallagher, 2005), or as a deficit of the body schema with a preserved body image (Coslett, 1998).

It is interesting to note that the way to assess personal neglect is by using exploratory actions like combing or shaving (McIntosh, Brodie, Beschin, & Robertson, 2000). It was also found that some patients with personal neglect were impaired in mental rotation for laterality judgments (Coslett, 1998). One may conclude that the representation of the left side of the body for action, namely, the body schema, is missing. What about the body image? The only reason why one would claim that the body image is impaired is that there is a lack of awareness of the left side of the body (Gallagher, 2005). This conclusion requires defining the body image in terms of consciousness. The argument would run as follows: the conscious body percept is missing, therefore, the body image must be missing. But one may easily imagine that patients with personal neglect have still their body percept, although they cannot have a conscious access to it. As far as *extrapersonal* neglect is concerned, it was shown that a patient was able to make judgments on burning houses presented in his left hemispace (Marshall & Halligan, 1988). Hence, he could make perceptual reports, although he was not conscious of the house. In this sense, his perceptual processing was preserved. As far as I know, there is no equivalent study for patients with *personal* neglect. However, on the basis of the findings on extrapersonal neglect, one may expect that patients with personal neglect will display the same type of performance and they will be able to make unconscious perceptual judgments about the left side of their body, although they are not aware of it. This would show a preserved perceptual body image. The body image, indeed, does not always need to reach the level of awareness.

Most probably, personal neglect is first an attentional deficit, before being a representational deficit (Kinsbourne, 1995). One may indeed notice that it is never a single body part that is neglected, as one would expect if it were a representational deficit. Similarly, there is no focal neglect in the visual field. Instead, it is the left side of the body that is neglected, especially its more extreme lateral parts (i.e. hands and feet). This could be explained by an attentional shift generated by a rightward bias, which can be reversed by vestibular stimulation (Cappa, Sterzi, Vallar, & Bisiach, 1987). From this point of view there is no need to postulate personal neglect as a deficit of body representation, i.e., neither a body image nor a body schema deficit. Rather it is a deficit of directing attention to the body. However, this attentional deficit must have consequences on body representations, on both the body schema and the body image. That it affects motor imagery is thus not surprising, especially since similar attentional effects have been shown in visual imagery too (Rode, Rossetti, Li, & Boisson, 1998). Surely it must have further consequences, still to be empirically investigated.

4.4. Autotopagnosia: semantic deficit, visuo-spatial deficit, or both?

Some patients are unable to localize body parts. Sometimes it affects localization on both one's own body and other people's body (and even pictorial body representations), sometimes only one's own body, and sometimes only someone else's body (Cleret de Langavant et al., 2009; Felician et al., 2003). Here I shall restrict myself to the inability to localize one's own body parts, namely, autotopagnosia. The good news is that there is some consensus that it results from a deficit of body image(s), although there is a little disagreement concerning the aspect of the body image that is affected, the visuo-spatial component (Schwoebel & Coslett, 2005) or the semantic component, or both (Sirigu et al., 1991). Patients with autotopagnosia have difficulties in constructing an image of a body with tiles. Although her performance was very poor, corresponding to that of a 4–6-year-old child, a patient reported being happy with the result, demonstrating she was unable to judge the oddity of her work (Guariglia, Piccardi, Puglisi Allegra, & Traballesi, 2002). In addition (except when autotopagnosia is associated with apraxia) patients are able to use the body parts that they cannot localize.

Yet, the diagnosis may not be so clear-cut. If the body image corresponds to the way we perceive our body and underlies our conscious body judgments, how is it possible that its impairment remained unnoticed? Patients with autotopagnosia are indeed not disturbed by their syndrome in their everyday life. They are not even aware that anything goes wrong. Furthermore, the most standard way of testing autotopagnosia is by showing that patients have difficulties to point to body parts. This is taken by Schwoebel and Coslett (2005) as an argument for a deficit of body image(s). Yet, as we have seen, pointing also potentially recruits the body schema, although less in the type of slow visually guided informative pointing used in the autotopagnosia studies. It would be interesting to also measure the spatial errors in blindfolded fast ballistic pointing movements.

4.5. *Numbsense and co: dissociation between action and touch*

Following cortical or subcortical lesions, patients with numbsense become completely anaesthetized on their right side. The tactile deficit can be so severe that the patient may cut or burn herself without noticing it. Even in verbal forced-choice condition, they cannot detect and they can neither verbally nor manually localize tactile stimuli (on a pictorial representation of the body). Yet, they can point to where they have been touched with their unstimulated hand, and to their own surprise (Paillard et al., 1983; Rossetti et al., 1995). In this sense, numbsense can be compared to what has been called action-blindsight (i.e. patients able to accurately act upon blind field stimuli by pointing or saccading towards them, although they cannot make visual judgments in a forced-choice condition) (Danckert & Rossetti, 2005). Interestingly, when numbsense patients were asked both at the same time to verbally localize and to point to where they had been touched, they became equally bad. Their bodily movements did not improve their performance in verbal localization. In addition, one patient with numbsense, JA, was unaware of his arm location. When his arm was passively moved while blindfolded, he could not verbally localize it. Yet, he was able to point accurately to the position of his arm (Rossetti et al., 1995). It thus seems that we have here a clear case of deficit of body image (impaired bodily judgments), with a preserved body schema (preserved body-oriented actions) (Paillard, 1999).

However, the dissociation between preserved actions and impaired detection judgments (conscious or not) shown in these patients has been recently challenged on methodological ground (Harris, Karlov, & Clifford, 2006). Briefly, patients were asked a "yes-no" judgment of detection. They thus had to adopt a decision criterion (i.e. when to say yes or no). In contrast, localization did not require adopting such decision criterion, and thus was more sensitive to whatever weak sensory signal was present to guide their movements. Harris and colleagues showed with healthy participants that if detection and localization were measured with equivalent forced-choice tasks, the subjects were unable to point to the tactile stimuli that they had not detected. The authors speculate that the dissociation between action and touch would disappear if this study were done with numbsense patients.

Yet, a recent study found a double dissociation between action and touch in localization tasks with identical decision criterion (Anema et al., 2009). Unlike numbsense patients, the patient JO can detect tactile stimulation on her right hand, although her sensitivity is decreased. She has no proprioceptive deficit. She was tested in four conditions. She was asked (i) to point with the unstimulated hand to the stimulated hand where she had been touched, (ii) to point with the unstimulated hand to a map of the stimulated hand, (iii) to point to neutral visual targets to control for perceptual and motor deficits, and (iv) to return her arm to the previously held position after it had been moved passively to a different location. It was found that she failed to point accurately to the hand map, whereas she did not fail to point to her own hand. Her difficulties with the hand map could not be explained in terms of visual or proprioceptive deficit, as she performed correctly in the two control tasks (iii) and (iv). Interestingly, the reverse dissociation was found in another patient, KE. Like JO, KE has preserved but decreased tactile sensitivity. Proprioceptive perception is damaged, but only partially and KE's performance in the proprioceptive task was similar to JO's performance. Using the same experimental paradigm as for JO, it was found that he failed to point accurately to his own hand, but not to the hand map. The double dissociation between JO and KE might be considered as the most convincing case for the distinction between body schema and the visuo-spatial aspect of the body image(s).

We have seen the difficulty in finding neuropsychological evidence for the functional distinction between body schema and body image(s). For some syndromes, there is no need to postulate a deficit of a specific body representation. They can be explained by external factors such as sensory or attentional deficits. Other syndromes, like apraxia and autotopagnosia, are quite plausibly due to impaired body representations. But how specific are the deficits? It seems that it is only in the case of the patients JO and KE that we eventually find a clear dissociation between the body schema and the body image(s). Unfortunately, we do not have much information about their lesions and their deficits. In addition, they must have at least a preserved sensorimotor representation of their pointing hand, which always successfully reaches the target in one of the two conditions (i.e. hand versus hand map). Let us see now if the dissociations are clearer in healthy individuals.

5. Dissociations in healthy participants

There may be more hope in validating the distinction between the body schema and the body image(s) in healthy individuals. However, very few studies have tried to dissociate the two types of body representation outside of neuropsychology (de Vignemont, Majid, Jola, & Haggard, 2009; Kammers, van der Ham, & Dijkerman, 2006; Kammers, de Vignemont, Verhagen, & Dijkerman, 2009; Tsakiris & Haggard, 2005). We have seen that one way of validating the Perception–Action model in vision is to show that action is not sensitive to some visual illusions like the Titchener's illusion (Aglioti, DeSouza, & Goodale, 1995). On the basis of such findings, although still controversial, one should expect the body schema to be immune to some bodily illusions such as the now classical Rubber Hand Illusion (RHI).

In the RHI paradigm, participants sit with their left arm resting on a table, hidden behind a screen. They are asked to visually fixate a rubber hand presented in front of them, and (with two paintbrushes) the experimenter simultaneously strokes both the participant's hand and the fake hand. After a short while, the majority of participants report that they feel the touch of the paintbrush in the location where they see the rubber hand touched. Even more surprisingly, they may feel as if the rubber hand were their own hand (Botvinick & Cohen, 1998). At the behavioral level, participants report their hand to be closer to the rubber hand than it really is. This is true only when the two hands are synchronously stimulated. In other words, vision 'captures' tactile sensations, and this multimodal match leads to proprioceptive drift.

The interest of the RHI is that it does not result solely from a pure temporal matching between visual and tactile information. Body representations also seem to play an important role (Costantini & Haggard, 2007; Tsakiris & Haggard, 2005). For instance, the effect of the illusion is reduced when the posture or the laterality of the rubber hand is incongruent with the unseen real hand. Consequently, the illusion should depend on the type of body representation that is recruited by the experiment. Most versions of the RHI mainly involve the body image, both because of the input (i.e. passive tactile stimulation) and because of the task (i.e. introspective report and perceptual judgment of the hand location). However, the body schema/body image(s) taxonomy predicts a dissociation between the subjective experience of the hand position and changes in sensorimotor coordination.

In Kammers, de Vignemont et al. (2009), after stroking the index finger (synchronously or asynchronously), we asked participants, who could no longer see the rubber hand nor their own hands, to indicate the felt position of their unseen stimulated hand by providing both verbal responses and motor responses. Several types of motor responses were used: (i) reaching the unseen stimulated hand with the contralateral hand (i.e. stimulated hand as the goal), (ii) reaching the contralateral hand with the unseen stimulated hand (i.e. stimulated hand as the effector), and (iii) grasping a stick with the two hands (i.e. object-directed action). We recorded the kinematics of all the motor responses. We found a proprioceptive drift for the perceptual response, but no proprioceptive drift for any of the motor responses. The kinematics of reaching movements towards the stimulated hand with the non-stimulated hand was similar after asynchronous and after synchronous stroking. The same was found for reaching movements towards the non-stimulated hand with the stimulated hand, as well as for grasping movements. In other words, the representations of the body both as the goal and as the effector were immune to the illusion.

Even more convincing, and maybe more surprising, is the independence of the perceptual and motor responses. When participants were asked a second time to give a perceptual judgment after having moved, they were still sensitive to the RHI. Visual information about the rubber hand location, which was available only during the stroking phase, remarkably kept on dominating despite the proprioceptive update following the movements of the stimulated hand. The dissociation between the two types of tasks is such that the RHI is maintained even after the motor response, which revealed an accurate sense of the position of the stimulated hand.

The results reveal a dissociation, but a dissociation between what? The verbal response most likely involves the body image(s). The question is whether the motor responses used in this study are action-oriented. Interestingly, in the original RHI study, Botvinick and Cohen (1998) asked participants to *point* where they felt their stroked hand was and they did find a proprioceptive drift. However, as acknowledged by the authors, the movements were not ballistic (Botvinick, personal communication). Although the participants did not receive visual feedback, they were allowed to make adjustments and to perform them slowly. By contrast, here we used reaching movements. As argued before, we believe them to be less ambiguous than pointing movements. The purely motoric function of the motor responses is even more convincing in the case of stick grasping. In all cases, participants made fast ballistic movements with no visual feedback. The results thus show that action-oriented responses do not follow the same rules as non-action-oriented responses in the sense that they are immune to the RHI. Participants knew how to get to their hand, but not where their hand was, even after having moved it. One may interpret these findings in terms of a dissociation between the body schema and the body image(s).

However, for the purpose of understanding the varieties of processing of bodily information, the distinction between perception and action is an unacceptable oversimplification, as shown by a further RHI study by Kammers, Kootker, Hogendoorn, & Dijkerman (submitted for publication). The hands (the participant's hand and the rubber hand) were shaped as if they were ready to grasp an object, with congruent or incongruent width of grip aperture. The index fingers and thumbs of both hands were stroked. After the stroking phase, participants were asked to grasp an object. It was found that the seen rubber grip aperture influenced the participant's maximum grip aperture during the grasping trajectory after synchronous stimulation only. It shows that some action-oriented motor response can be affected by bodily illusions. This result is in line with the well-known dissociation between visually guided movements of reaching and grasping (Jeannerod, 1997). Reaching and grasping components of prehension reflect the output of two independent, though temporally coupled, motor programs (Jakobson & Goodale, 1991; Roy, Paulignan, Meunier, & Boussaoud, 2006). For instance, a patient with bilateral posterior parietal lesion showed a deficit in grasping objects, with no deficit in reaching them (Jeannerod, 1997).

Do these new results challenge the previous ones by Kammers, de Vignemont et al. (2009)? No. It is true that action is affected by the rubber hand in this study, and not in the former. However, it was the hand trajectory that what was recorded in the former, and the maximum grip aperture in the latter. Yet, it remains that some aspects of action calibration can be sensitive to the RHI, in the same way that they were found to be sensitive to visual illusions in some contexts (Franz, Gegenfurtner, Bulthoff, & Fahle, 2000; Smeets, Brenner, de Grave, & Cuijpers, 2002). There seems to be no longer a difference with non-action-oriented responses. Should we then give up on the distinction between body schema and body image(s) if the evidence is so dim and limited? I would like to suggest here that these last results about grip aperture are more an invitation to refine our model than a decisive objection. They do not show that there is only one type of body representation. What they really challenge is the hypothesis that the two types of body representation work independently in complete isolation in healthy individuals. But nobody is ready to defend such an extreme view. Most likely, the body schema and the body image(s) interact all the time. This is what we have already seen with neuropsychological disorders, which almost never affect only one type of body representation. This interaction is also what could explain the effect of the RHI on grip aperture. Hence, it is necessary to move beyond an absolute dichotomy between perception and action and to investigate when and how the body schema and the body image(s) work hand in hand. In order to do so, one needs more experimental evidence, but also a computational model of how body representations are built up.

6. Building up body representations

The neuropsychological taxonomies on body representations focus primarily on the final output of bodily information processing, neglecting prior computational stages. They offer no explanation of the principles governing the construction of body representations. We might be able to shed a new light on the distinction between body schema and body image(s) by investigating how they are built up at the computational level (Kammers, Mulder, de Vignemont, & Dijkerman, 2009).

We continuously receive a flow of sensory information about our own body, from various sources. All these different sources of information interact with each other to build up body representations. They can interact in two different ways. We must distinguish between *sensory combination* and *sensory integration*, which both participate in body representations formation (Ernst & Bülthoff, 2004). Sensory combination describes interactions (e.g., cooperation and disambiguation) between sensory signals that are not redundant. By contrast, sensory integration describes interactions between redundant signals. To be integrated, the sensory estimates must be in the same units, the same frames of reference and about the same aspect of the body. They can then be efficiently merged to form a coherent and robust body representation.

There are thus three main obstacles to overcome. First, the relevant elements to integrate as a single body percept must be selected and segregated from those belonging to other bodies or objects. There is always the risk indeed that one integrates signals from one's own body with signals from someone else's body, or even from a rubber hand. How to guarantee that the different channels of sensory information come from a common source? The second problem is a Tower of Babel type of problem. Each sensory modality is encoded in its own spatial frame of reference. Consequently, the brain cannot just combine and average the converging sensory inputs. More elaborate computations are required. How to go beyond the differences between sensory formats and spatial frames of reference? The third problem is that all the sensory inputs are not equally trustworthy, and their respective reliability varies widely according to the context and the type of information. How to temper the importance of each modality given the context? This latter question is at the core of Bayesian models, which provide a set of rules to optimally combine sensory inputs with varying reliabilities (for review, see Mamassian, Landy, & Maloney, 2003; Pouget, Deneve, & Duhamel, 2002).

A Bayesian model starts with some a priori knowledge about how a system should work given biological and environmental constraints. It is represented by a prior probability distribution for a model's structure and parameters—what the variables are and how they influence each other. For example, it represents the relative plausibility of different locations of the hand. It aims at computing the posterior probability, that is, the degree of belief in the prior hypothesis conditioned on the observation of sensory evidence. The posterior probability is proportional to the product of the prior probability and the likelihood function. The likelihood is the probability of the data given the hypothesis. It represents everything one knows about the process that turns the state of the world into sensory information. Once the posterior probability computed, the system has an estimate of the hand position for instance. The decision made by the system about the hand location, whether it results in a motor act or a judgment, however, requires further computations using gain and loss functions. For every decision, there are consequences that depend upon the true location of the hand, consequences that can be positive or negative. The Bayes decision rule aims at maximizing the expected gain given the posterior probability.

What is interesting with Bayesian models is that they provide a model of understanding of how the functional role can affect the content of body representations. Bayesian models show that the formation of body representations is task-dependent. The respective weight of the inputs varies relatively to the variability of the cues and the variability of each cue depends on the context. Not only the weight given to the sensory signals can vary, but also the decision-making rules with different gain and loss functions, and this again depends on the task. One may thus speculate that whether the task is action-orientated or not, it appeals to different prior knowledge leading to different weighting of information. In addition, one may speculate that the consequences of the decision for a motor task might differ from those for a perceptual task. For instance, it would be more important to be more accurate for action than for perception. If so, the decision criteria would differ and this would lead to two distinct types of body representations, those that are action-oriented and those that are not.

7. Conclusion

What is the functional organization of the representation of the body? I have analysed here the distinction between the body schema and the body image, a distinction that owes much to the Perception–Action model of vision. And like the dual model of vision, the distinction between two functionally defined types of body representation is controversial. Deficits of body schema and deficits of body image(s) are often intermingled within the same syndrome and hard to take apart, except in few cases. The lack of clear dissociation in these syndromes should encourage us to clarify the notions of the different types of body representations and to emphasize the interaction between them. Even the notion of the body schema, unto which there seems to be a more widespread agreement, is victim of conceptual confusion. But if one analyses what is required by action guidance, then one can offer a clear definition. I proposed here that the body schema is better conceived as a cluster of sensorimotor representations that are action-oriented. It represents the body both as the effector and as the goal of the action, including short-term and long-term bodily properties that are relevant for action programming, action prediction and sensory feedback. In addition, sometimes, but not always, the body schema obeys principles that are different from those that apply to non-action-oriented body representations, like in the RHI.

Because these representations serve different purposes, they have different contents. The way we use bodily information determines the way the brain encodes it. Interestingly, this principle is at the core of the prominent Bayesian approach, which has been applied to a broad spectrum of cognitive abilities, including multimodal integration. By studying how tactile, proprioceptive, visual, and vestibular sources of information are integrated, one may be able to understand how the brain represents the body and how it represents it in a different way depending on its functional role. I suggest here that the Bayesian framework offers a useful dynamic model of body representations and of their task-specificity. However, one should not confuse the Bayesian approach with a purely bottom-up approach based solely on raw sensory data. On the contrary, the Bayesian models highlight the importance of what they call prior knowledge, which puts higher-level constraints on multisensory integration. Much remains to be investigated about the psychological nature and content of bodily prior knowledge. Yet, the Bayesian approach allows going beyond the dichotomy between bottom-up and top-down approaches by integrating the two.

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