Historically, the first study speculating about the existence of a representation of body’s orientation was authored by Munk (1890), who argued that vivid multisensory images of former sensations are able to maintain a stable representation of the body in space despite a persistent continuous variation of the sensory inputs on the skin. These images were held to occur at the very early stages of life as a consequence of first reflexes and motions. Small lesions of the sensorimotor cortex were expected to produce the loss of images for specific body parts.

Subsequently, these ideas were developed by Wernicke (1906), who postulated that a deep correspondence exists between cells in the sensorimotor cortex and sensory organs. Wernicke argued that the signals sent from different body parts are qualitatively different from each other, and that the cortex, which is able to distinguish between these "qualities", could build a stable image of each body part in the space, by merging all the signals together. The integration of these signals was supposed to build up a giant image of the overall body, called "body consciousness" or "somatopsyche". Interestingly, in Wernicke’s theory these images are proportional to the distribution of receptors on the sense organs. These theories are consistent with the cultural framework they were developed within, when the body awareness was understood as a bottom-up phenomenon generated by the integration of multiple sensations arising from muscles, viscera, joints, skin, etc. (Poeck & Orgass, 1971).

A different viewpoint was brought forward by Bonnier (1905), who described several patients suffering from labyrinthine vertigo. These patients reported their body parts as being absent, smaller, bigger or misallocated with
respect to their actual positions. Bonnier ascribed these deficits to specific disorders of the topographic schema of the body. He classified the patients as cases of hyper- or hyposchématie, that is patients with the illusory over- or underestimation of the size of the whole body (or of parts of it). He also classified as paraschématie the illusory perception of some body parts as drifted from their original position. Finally, he reported cases of aschématie, whereby patients showed a strong inability at localizing the boundaries or the postures of their own body. Bonnier’s work has been strongly criticized because his description of the deficits was not clear (Vallar & Papagno, 2003). Bonnier no doubt deserves the merit of having hypothesized the existence of a spatial schema of the body rather than considering patients as affected by psychiatric disorders.

The notion of schema will be found again in the studies of Head and Holmes (1911). The authors describe a mechanism that integrates the sensations arising from different sensor modalities into an online dynamic model of our own actual posture. With the term schema (or schemata), the authors referred to a comparison between two sequential sensory inputs, providing information about the changes of posture rather than on the posture itself. Head and Holmes argued that one of their patients was lacking the postural schema in that he was unable to report the position of his own hand while still able to localize the position of a perceived tactile spot. From this dissociation they concluded that the schema based on the body posture should be different from that of the skin surface, and they called the latter superficial schema. The authors also distinguished the notion of schema from that of image (frequently used by Munk and Wernicke): they considered an image of the body as an explicit representation, while the schema was regarded as a pre-conscious organized model against which all postural changes are measured.

The theories brought forward by Head and Holmes (1911) are traditionally linked to the work of Pick (1908, 1922) who is credited with the first description of autotopagnosia (1908) as the inability to locate body parts at command within an entire body structure. However, whereas Head and Holmes developed an enduring model that is still discussed nowadays (e.g. Lackner, 1988; Sirigu, Grafman, Bressler, & Sunderland, 1991), Pick is rather known for his famous clinical studies. Moreover, his ideas were largely inspired by Munk and Wernicke, and even when he borrowed the term schema (Pick, 1915) he was not keen to accept the hypothesis of an automatic preconscious representation, à la Head and Holmes (1911).

The name autotopagnosia, that means lack of knowledge about one's own space, was attributed by Pick (1908) to someone’s deficit in pointing at the correct body part on command, irrespective of whether the body was his own or
someone else’s. Gerstmann (1942) proposed the term somatotopagnosia (literally lack of knowledge about the body space), a name that is still frequently used, to stress the fact that this deficit involves a general notion of body and not simply of the patient’s own body.

It was Gerstmann (1922) who brought about the notion of Body Schema (hereafter BSc) in describing a patient affected by finger agnosia, right-left disorientation, agraphia, and acalculia. The calculation and writing deficits were originally attributed to finger agnosia but, later, Gerstmann (1942) argued that the locus of the patient’s deficit was in the Body Schema, and that his problem involved in particular the ability to recognise, identify, name and orient fingers of either hand (his own and of others). This pattern of deficits, called Gerstmann syndrome, is often observed in patients with a lesion of the left angular gyrus, which is still considered one of the most frequent anatomical correlates of autotopagnosia (see Vallar & Papagno, 2003, for a review).

The notion of a BSc as a unitary monolithic concept was introduced by Schilder (1923), who combined a great variety of neuropsychological symptoms seemingly related to the orientation of one’s own body. Schilder postulated the existence of a three-dimensional spatial image that everybody has of him/her self, neglecting Head and Holmes’s view (1911). He also added a psychoanalytical interpretation of the libidinal structure of the image of the body (Schilder, 1935).

In the Fifties, the notion of BSc was generally accepted (Benton, 1959; Riese & Bruck, 1950; Wright, 1956) but there was only a weak agreement about the nature of the representation, internal structure and putative subdivisions. The debate mainly focused on the conscious nature of the body representation: an implicit and automatically working schema rather than a conscious cluster of sensory images. This distinction between Bonnier’s and Head’s interpretation, and that proposed by Munk and Pick is still present in recent models, although the names referring to their concepts have changed.

Is autotopagnosia simply a loss of spatial abilities?

Since Pick’s seminal studies on autotopagnosia (or, after Gerstmann, somatotopagnosia), several cases of disturbances of the BSc have been reported (Engerth, 1932; Hécaen & Ajuriaguerra, 1952; Semmes, Weinstein, Ghent, & Teuber, 1963) However, in some reviews it was suggested (De Renzi & Scotti, 1970; Poeck & Orgass, 1971) that most of the results described could be due not to a pure damage of the body representation, but to aphasia or spatial deficits. Even the patient originally studied by Pick’s showed, together with an impairment in the pointing task, severe memory deficits, and other mental
disorders. Other patients were described as having difficulties in naming body parts, although they could perform the pointing task normally (Selecki & Herron, 1965), raising the doubt that the patients were aphasic rather than autotopagnosic (Poeck & Orgass, 1971). As to the spatial deficits, De Renzi and Scotti (1970) described a patient who was severely impaired at pointing to body parts on verbal command, even though he was perfectly able to name them. However he was unable to point components of complex objects but maintained the intact ability to pronounce their name. This case revealed that many patients with severe problems at pointing to body parts could have an intact body representation, at the same time showing severe deficits when analyzing parts of an arbitrary object.

Autotopagnosia is an rather rare neuropsychological deficit, that occurs in conjunction with many others (Poeck & Orgass, 1971). The case described by De Renzi and Scotti (1970) demonstrated that many cases found in literature could be explained by deficits other than autotopagnosia. It is therefore possible that, until then, a pure case of autotopagnosia had never been found. Following De Renzi and Scotti’s (1970), a patient is diagnosed as having autotopagnosia if he/she show the following features:

1. A selective deficit in processing the spatial characteristics of the human body only.
2. A supramodal deficit in locating body parts that persists in all input (e.g. verbal vs. visual command) and output (e.g. verbal vs. motor response) modalities.
3. A deficit that shows up not only when pointing to one’s one body, but that also to a line-drawing of the human body (see Semmes et al., 1963).

The first patient matching the above characterizations was a 59-year-old man affected by a metastatic carcinoma in the left parietal cortex (Odgen, 1985). Even though he was perfectly able to name body parts and to specify their functions, he was grossly impaired at pointing at them, irrespectively of whether the body was his own, the examiner’s, a line-drawing (Semmes et al., 1963) or a doll. This impairment lasted even when the patient was asked to imitate the examiner’s pointing. However, he was perfectly normal at pointing to parts of a toy truck and of a vase.

Odgen (1985) interpreted the patient’s as a disruption of a "discrete body image" (p. 1020) caused by a lesion in the left parietal cortex. This deficit cannot be interpreted as an inability to decompose an arbitrary object into its parts, nor as a conceptual lack of explicit knowledge of body parts. Even though Odgen’s study can be considered the first documented case of pure autotopagnosia, the author described several errors the patient committed when
performing spatial tasks involving body parts, without analysing the nature of these errors. Such an analysis was later performed by Semenza (1988) and by Sirigu et al. (1991).

**Multiple representations of the body**

Sirigu and colleagues (1991) described the case of a 62-year-old patient, DLS, with a probable dementia of Alzheimer, who showed a Gerstmann syndrome and severe visuospatial deficits. Like the patient studied by Odgen, DLS failed at pointing to single body parts within an entire body structure and made more contiguity (e.g. elbow → shoulder) than conceptual (e.g. elbow → knee, toe → thumb, etc.) errors. However, she was perfectly able to recognize and name these parts when presented in isolation, as well as to provide a detailed description of their function. In the pointing task, the patient was able to locate small objects (e.g., cars, soldiers) taped on the examiner’s and patient’s body parts; yet, she could point at these objects on verbal command or on imitation. DLS was also able to remember the locations after a delay of 24 hours.

Based on these observations, Sirigu et al. (1991) proposed the existence of three main levels of body knowledge: the first is the semantic knowledge about body parts (body semantics - hereafter BSe); the second is the Body Schema (BSc) proposed by Head and Holmes (1911), a dynamical body-reference system that provides the information about the subject’s body in space; the third is a visuo-spatial map of the body which provides a description of the spatial arrangement of the body segments and of the junctions between them. The latter representation is the one that seems to be deficient in Sirigu’s patient, since she could not point at body parts within the context of an overall body, though she was perfectly able to: i) recognise those body parts in isolation, ii) locate sub-parts on the structure of a non-body object, and iii) perform pointing movements over her own body (when the task did not require aiming at her body parts).

Sirigu et al.’s (1991) account was mostly speculative, as they provided only evidence of a selective damage of the visuo-spatial map of the body, but not of the other levels namely BSc and BSe, with spared visuo-spatial representation.

However evidence in support of a multiple-level representation of the body proposed by Sirigu et al.’s (1991) was brought to bare by the extensive work of Buxbaum, Coslett and collaborators (Buxbaum & Coslett, 2001; Buxbaum, Giovannetti, & Libon, 2000; Coslett, Saffran, & Schwoebel, 2002) who described patients with a selective damage affecting one representation at a time.
What the Brain knows about the Body: Evidence for Dissociable Representations

Body structural description

Buxbaum and Coslett (2001) described the case of a patient, GL, with a strong left fronto-parietal trauma, who was severely deficient in pointing to body parts (but not to animal and object parts) on verbal command or imitation, as well as in matching pictures of the body parts across shifts in perspective. In contrast, GL was able to scale his grasp appropriately in object-oriented actions and to localize objects taped on the body surface. His performance improved when he was cued with semantic information about the body parts he had to locate. The authors concluded that GL’s damage involved the visuo-spatial map of the body, which they call "body structural description" (hereafter BSd), and that both the BSc and the explicit semantic knowledge about the body (BSe) were intact. Moreover they argued that the BSd defines the relative positions of body segments in a perceptual format and independently of potential transformations in orientation. They also suggested that the BSd is located in the left posterior parietal cortex.

Dynamic representation

Buxbaum et al. (2000) discussed the case of a patient, BG, with apraxia (i.e. deficit in pantomiming to verbal command or on imitation), who had difficulty in gesturing to command or imitation (except when using tools), in matching gestures, especially when a spatial transformation was required, and in performing mental motor transformations of body-parts stimuli. The authors concluded that the patient’s deficits in pantomiming, recognition, and imitation resulted primarily from deficits in the dynamic coding of intrinsic positions of the body parts of self and others (i.e. BSc). This finding is consistent with what Coslett (1998) observed in a group of patients with unilateral left or right hemisphere lesions, who were asked to decide if photographs depicted a right or a left hand. In order to accomplish the task, participants have to imagine their own hand to rotate until it matches the stimulus (Parsons, 1987), with temporal and kinematical properties of mental images mimicking those of the real hand movements (Parsons, 1994). Coslett observed that only hemi-neglect patients (who had a lesion on the right angular gyrus) were impaired when photographs depicted the contralesional left hands. In fact, left-hemisphere patients or right-hemisphere patients with lesions sparing the angular gyrus did not show any specific deficit. The author concluded that neglect patients seem to be unable to access the hemi-portion of their BSc, and he also suggested that the left hemisphere may contain the structural description for both sides of the body, whereas each hemisphere may predominantly represent the postural potential transformations for the opposite side, as it is the case for the motor system.
Suzuki, Yamadori, and Fujii (1997) reported a patient with Broca’s aphasia who exhibited impaired body part name comprehension despite preserved comprehension of words from other semantic categories, and a preserved ability to point to visually identified body parts on himself. By contrast, Coslett et al. (2002) reported the case of a patient, who exhibited semantic dementia, with selective preservation of body part semantic information despite impaired comprehension of words from other categories. Moreover this patient performed well on: i) tasks involving mental transformations of body parts and ii) the same pointing task used to test autotopagnosic patients. Similarly to the early work done by Semenza and Goodglass (1985), Coslett et al. (2002) hypothesized the existence of a third representation containing the conscious lexical-semantic knowledge of the body parts (i.e. the BSe or body image).

Likewise Sirigu et al. (1991), Buxbaum, Coslett and colleagues also suggest the presence of three distinct kinds of body representations, the pre-conscious BSc and BSd and the lexical conscious BSe (or lexical conscious "image" of the body), and that each can be selectively damaged by a lesion. More recently, Schwoebel, Buxbaum and Coslett (2004) used the influential multiple routes model of action production (Gonzales-Rothi, Ochipa, & Heilman, 1991) to draw predictions about the body representations expected to tap the production and the imitation of meaningful and meaningless gestures. Using a multiple regression analysis, they showed that the performance of 55 left brain damaged patients during the imitation of meaningless movements was highly correlated with the performance on the hand laterality task (Parsons, 1987), but not with that on the pointing task (Buxbaum & Coslett, 2001; Odgen, 1985; Sirigu et al., 1991) or on a semantic task involving body parts (i.e. matching body parts on the basis of their functions). Conversely, patients’ ability to imitate meaningful movements correlated with the performance on both the hand laterality and the semantic task, but not with the performance on the pointing task. According to Schwoebel, Buxbaum, and Coslett (2004), the spared performance on the semantic task, supposedly tapping the BSe, was a good predictor for the spared "semantic route" only, whereas the performance on the laterality task, which was held to tap the BSc, was related to both "direct" and "semantic" routes.

Deficits on the BSc may affect the imitation of both meaningful and meaningless actions, suggesting that the BSc is a dynamic model of the positions of the body parts of self and others in space, which is activated irrespective of the fact that the gestures to be imitated are computed by the semantic or by the direct route. On the other hand, the BSe is related to the imitation of meaningful gestures only, confirming that BSc and the BSe are dissociable representations (see Figure 1).
Similar results were obtained in a group study by Schwoebel and Coslett (2005) who administered to 70 stroke patients a battery of tests including: a handedness task (Parsons, 1987b), that assesses the ability to mentally rotate one's own body part; a matching body parts by function (e.g. "which body part has the same function of an elbow?" - "a knee"), to clothing or to objects (e.g. "which of the following clothings is mostly associated to a leg?") tasks; a pointing task similar to the one clinically used to assess autotopagnosia; a task in which patients' real hand movements were compared with their imagined movements in order to assess their ability to simulate actions (Sirigu et al., 1996). The authors found that thirteen patients were impaired in either the hand laterality or the real/imagined hand movement task, but performed normally on both the pointing and the matching tasks. Moreover three patients were found impaired in the matching task only, whereas two patients showed a selective deficit in the pointing task. Thus, Schwoebel and Coslett (2005) concluded that BSc, BSe and BSD are independent and dissociable body representations.
Figure 1: Model representing the difference between three different levels of body knowledge and multiple routes of action production (Schwoebel et al., 2004).
Does autotopagnosia express a faulty body representation?

Buxbaum and Coslett’s viewpoint is not free from criticism. First of all, it does not explain clearly the role of the BSd, described as a representation that specifies the spatial relations among of body parts on a standard body (Buxbaum & Coslett, 2001; Sirigu et al., 1991). It remains to be clarified whether this is a visuo-spatial representation enriched by visual experience of human bodies in everyday life (Slaughter & Heron, 2004) or a top-down representation integrating inputs from different modalities in order to generate an on-line representation of the body in space (i.e. the BSc). The representation of the body shape and posture can be manipulated by mechanically vibrating muscle tendons. Goodwing, McCloskey and Matthews (1972), for instance, induced an illusory motion of a stationary limb, and Lackner (1988) was able to induce a vivid sensation of physically impossible body conformations and of abnormal body dimensions. These results clearly show the influence of top-down constraints in constructing the BSc. According to this hypothesis, a damage of the BSd should always be associated with a faulty BSc. In particular, if the BSd is involved in updating the BSd, the autotopagnosic patients with a putative selective damage of the BSd should have difficulties in perceiving their own posture. This prediction is inconsistent with the proposal of Buxbaum and Coslett (2001) that the BSd and BSc could, in principle, be independently damaged. To date, Denes, Cappelletti, Zilli, Porta, and Gallana (2000) suggested that autotopagnosia (Odgen, 1985; Sirigu et al., 1991) may not express a faulty body representation but an inability to bring to awareness the detailed representation of the spatial relations among body parts. Evidence supporting this view comes from the fact that, in real life, these patients do not show any kind of neglect or inability to reach the various parts of their body, even in tasks that require fine grained spatial location of the body parts, such as putting the make-up or shaving.

Hetero- and Autotopagnosia

One of the most peculiar features of autotopagnosia is that patients fail to point to the correct body part on verbal command, irrespective of whether it is their body or someone else’s. Based on this observation, it has been proposed that the BSd is supramodal. Likewise, Reed and Farah (1995) showed that healthy participants were faster in making visual judgments concerning body parts of others when they moved their own corresponding body part, suggesting that the Body Schema refers to an abstract representation of the body structure.
which sustains the spatial knowledge of one's own body as well as that of others.

Denes et al. (2000) administered Reed and Farah's (1995) test to two aphasic patients, with a lesion of the left posterior parietal and right temporo-parietal cortex respectively. They found that both patients were unable to point to body parts on themselves or on a mannequin, and that they were worse than controls on a same-different matching task for body positioning (Reed & Farah, 1995), but not for non-body Lego blocks figures. One weakness of this study is that the authors argued that in the right brain-damaged patient the body representation is represented together with his language functions in the damaged hemisphere. However, Denes et al. (2000) clearly showed that both the ability to locate body parts within the whole body (i.e. the pointing task used to diagnose autotopagnosia) and that of detecting changes of body positions in a model (i.e. the experiment carried out by Reed and Farah, 1995) are closely linked.

Felician, Ceccaldi, Didic, Thinus-Blanc, and Poncet (2003) recently claimed that the BSd might not be an abstract representation that codes information about one's own body as well as of others. They described a double dissociation between a deficit in pointing at their own body parts and that of pointing at body parts of others in two patients. In particular, these authors described two patients (respectively 73- and 68-year old) suffering from a neurodegenerative disorder. The first patient, with a lesion involving the left superior parietal lobule and the superior portion of the angular gyrus (Brodmann areas 7 and the superior part of 39), showed an inability to report the positions of his body parts when passively moved by the examiner as well as to point to his own body parts. In contrast, semantic and explicit knowledge about the body parts' and body structure was preserved, from naming to giving definitions, as well as her ability to point to parts of a line-drawing human, a mask and the examiner's face. The second patient, with a lesion of the left inferior parietal lobule and angular gyrus (Brodmann areas 39-40), had neither apraxia nor a proprioceptive disorder; her semantic knowledge about the body parts' function was preserved, whereas she was unable to report verbally how body parts were spatially arranged¹; finally she did not benefit from the perception of the examiner's body. More importantly, she was as good as controls in performing a pointing task on her own body, but she was unable to point at examiner's parts, unless she was requested to aim at little objects taped on his body, as previously showed by Sirigu et al. (1991).

At variance with Buxbaum and Coslett (2001), Reed and Farah (1995), and Denes et al. (2000) who suggested the existence of an independent, unitary

¹ In this the patient was asked whether a shoulder is above or below a knee.
visuo-spatial system devoted to the processing of both one’s own and other bodies, Felician et al. (2003) argued that this system may be related only to the body of others, that could be damaged by a lesion of the left angular gyrus, hence generating heterotopagnosia. Rather the information of one’s own body is processed in the superior parietal cortex, normally thought to be dedicated to process somatomotor aspects of the body. Pointing to body parts may involve many unimodal representations of the body each of which could be selectively damaged.

Conclusions

Can the notion of Body Schema still be considered as a unitary concept? Neuropsychological studies with autotopagnosic patients seem to suggest that this is not the case. Yet, it is not clear how many levels this representation should have. The original distinction between the implicit, automatic functioning schema, and a conscious visual image has been reconsidered. Some authors (Schwoebel et al., 2004) have suggested that the body image can be referred to as the semantic explicit knowledge of bodily facts (BSe), whereas new views have proposed an additional subdivision within the schema. Thus the traditional concept of a dynamical representation of one’s posture (BSc) became distinct from a visuo-spatial representation of a static body (BSd), with the former being strictly related to one’s body structure, and the latter being a more general representation which can also sustain (or, according to Felician et al., 2003, which relies exclusively on) the processing of other people body (Buxbaum & Coslett, 2001).

References


What the Brain knows about the Body: Evidence for Dissociable Representations


**Author Note**

We would like to thank Leone Corradi and Emily Kuria for resuming the manuscript.