Multimodal Contributions to Body Representation

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Abstract

Our body is a unique entity by which we interact with the external world. Consequently, the way we represent our body has profound implications in the way we process and locate sensations and in turn perform appropriate actions. The body can be the subject, but also the object of our experience, providing information from sensations on the body surface and viscera, but also knowledge of the body as a physical object. However, the extent to which different senses contribute to constructing the rich and unified body representations we all experience remains unclear. In this review, we aim to bring together recent research showing important roles for several different sensory modalities in constructing body representations. At the same time, we hope to generate new ideas of how and at which level the senses contribute to generate the different levels of body representations and how they interact. We will present an overview of some of the most recent neuropsychological evidence about multisensory control of pain, and the way that visual, auditory, vestibular and tactile systems contribute to the creation of coherent representations of the body. We will focus particularly on some of the topics discussed in the symposium on Multimodal Contributions to Body Representation held on the 15th International Multisensory Research Forum (2015, Pisa, Italy).

Introduction

Our body is an essential component of our sense of self and what we use to interact with the external world. We carry our bodies everywhere in every moment of time, and as a consequence, we are all constantly and inevitability confronted with bodily-related information (Bermúdez, Marcel, & Eilan, 1995). Bodily sensations originating from the skin surface or from the vestibular and proprioceptive senses contribute major information about the way we are constituted as an individual (Longo, Azañón, & Haggard, 2010). For instance, they provide information about the structural relations of our body parts, such as location and posture of our limbs at a given moment in time. Importantly, these sensations constitute just one source of bodily-related information. As we move through and explore our world, we are also exposed to informative visual inputs about the appearance of our bodies. Similarly, we are exposed to auditory signals that originate from our body. These signals do not only provide information about the length and thickness of our bodies, but also about our internal states, such as those related to heart beat and respiration (Gibson, 1966). All these inputs are combined to construct the large variety of body representations that we have (de Vignemont, 2010; Schwoebel & Coslett, 2005). These representations include, for instance, those related to what we perceive our body as being like, but also the knowledge we have about bodies in general or the emotions and attitudes that may be directed towards one’s own body (Longo et al., 2010) .

The way in which we represent our body strongly relies on this inflow of inputs from different sensory modalities and, critically, on how they are integrated. A well-known example of these interactions is the “Rubber Hand Illusion” (Botvinick & Cohen, 1998). In this classical experimental paradigm, participants observe a rubber hand being stroked while their unseen real hand is also touched in synchrony. After several seconds of synchronous stroking, participants tend to perceive the location of their own occluded hand misplaced toward the rubber hand (Tsakiris & Haggard, 2005). Participants also tend to perceive the felt tactile sensation originating from the rubber hand, as if they could experience touch through it (Pavani, Spence, & Driver, 2000), which generally results in a feeling of ownership over the fake hand (Longo, Schüür, Kammers, Tsakiris, & Haggard, 2008). This illusion is a clear example of the *plasticity* of body representations. The cross-modal temporal correlations between vision and touch, along with top-down influences originating from the representation of one's own body, leads to the quasi instantaneous incorporation of a fake hand into the body representation (Tsakiris & Haggard, 2005). The critical role of inputs from the different senses to this illusion is supported by neuroimaging studies in humans in which activity in multisensory brain areas has been found to be associated with the illusion (Ehrsson, Holmes, & Passingham, 2005; Ehrsson, Spence, & Passingham, 2004; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007).

Given the multisensory nature of body representations, it is difficult to isolate the relative contributions of each modality to the formation of a coherent bodily self. This review aims to provide an overview, though non-exhaustive, of the most recent evidence of the contribution of the different sensory modalities to body representation. Specifically, we focused on the topics discussed in the symposium titled *"Multimodal Contributions to Body Representation"* (15th International Multisensory Research Forum, 2015, Pisa, Italy). We will start by describing the contribution of vision, which provides us a generous amount of information in specifying the relative proportions of our body. In this respect, it has been shown that there are large distortions in the visual perception of the relative lengths of individuals' bodily proportions. We will discuss the origin of these distortions as well as their role as a compensatory mechanism to achieve a reasonable degree of tactile constancy despite differences in tactile receptive filed sizes across the body. In the next section we will describe how similar distortions emerge also when the sensory input is tactile. In a further section, we will provide behavioural demonstrations that vestibular signals contribute to bodily awareness modulating the weighting of other sensory signals in the process of multisensory integration of information about the body. We will also discuss how sounds that accompany almost every of our bodily movements are used to form body representations. Finally, we will explore how vision of the body modulates the perception of pain and discuss the role that some aspects of body representation, such as body ownership, has in maintaining intact responses to painful stimuli. The review will end with a concluding remark of the current state of the art of research on sensory contributions to body representations and proposals for future investigations.

Visual contribution to body representation

Unlike the perception of non-corporal objects, which can also be perceived by one modality in isolation, the body is always experienced via sensory inputs from several modalities. However, in humans, vision has traditionally been considered the dominant sense as well as the most reliable in terms of spatial perception (Power & Graham, 1976; Rock & Victor, 1964).

Several studies have shown that vision, and in particular, visual information about the body, influences body representations at several stages of processing. For instance, non-informative vision of a body part, but not of a neutral object, seems to improve tactile spatial resolution at that body part (Kennett, Taylor-Clarke, & Haggard, 2001; Konen & Haggard, 2014; Longo, Cardozo, & Haggard, 2008; Press, Taylor-Clarke, Kennett, & Haggard, 2004; Taylor-Clarke, Jacobsen, & Haggard, 2004; Tipper et al., 1998, 2001), affect somatosensory intra-cortical inhibition (Cardini, Longo, & Haggard, 2011) and modulate tactile size perception (Longo & Sadibolova, 2013), amongst other effects (e.g., Serino, Farnè, Rinaldesi, Haggard, & Làdavas, 2007). These results suggest that higher visual representations of the body interact with the neural circuits devoted to tactile processing. Seeing the body has also shown to produce limb-specific modulation of skin temperature (Sadibolova & Longo, 2014), suggesting a modulatory effect of vision on the autonomic system. Moreover, seeing a body part in a certain position affects the location where we perceive touch (e.g., Azañón & Soto-Faraco, 2008; Gallace & Spence, 2005; Soto-Faraco, Ronald, & Spence, 2004) and visual experience during development seems to shape, more generally, the way in which touch will be processed in adulthood (Nava, Steiger, & Röder, 2014; Röder, Föcker, Hötting, & Spence, 2008; Röder, Rösler, & Spence, 2004).

As mentioned above, vision can also have striking effects in situations such as the rubber hand illusion (RHI), where a tactile-proprioceptive conflict is introduced (Botvinick & Cohen, 1998; Tamè, Farnè, & Pavani, 2013). Interestingly, the RHI only occurs when the rubber hand is placed in an anatomically plausible position (Pavani, Spence, & Driver, 2000; Tsakiris & Haggard, 2005), which suggest that this phenomenon is modulated by top-down signals that originate from the visual representation of one's own body (see also Pavani & Zampini, 2007). Furthermore, this illusion can be induced as a full-body experience, with the feeling of “global ownership” of another body (studied in the full-body illusion; for a review see Blanke & Metzinger, 2009). Interestingly, blind and sighted individuals perform differently in a somatic version of the rubber hand illusion. Sighted participants experience a strong illusion, whereas blind individuals do not, when measured with a questionnaire (Nava et al., 2014; Petkova, Zetterberg, & Ehrsson, 2012), suggesting a contribution of vision in shaping the way we perceive our bodies to be. One hypothesis is that the lack of vision both during development and adulthood provides a more “veridical” percept of self-touch and a less flexible representation of their own body in space (Petkova et al., 2012).

These studies, which span just a limited range of examples in the literature, demonstrate the impact that both developmental and online visual information has in modulating the representation of our own body. These reports assume that vision of the body is accurate, however, recent evidence suggest that this may not always be the case - visual perception of one’s body dimensions can be highly distorted in some situations (Linkenauger et al., 2014). The rest of this section will focus on this evidence.

In a recent study, Linkenauger and colleagues (2014) have found that neurologically intact individuals have large distortions in the perception of their own body proportions, even when looking at their bodies in a mirror (Linkenauger et al., 2014). Specifically, when using the hand or foot as a metric to estimate the lengths of their body parts, people tend to overestimate the size of each body part, but not of corporeal objects (such as a body-size cylinder), in a systematic manner (Linkenauger et al., 2014). Moreover, the magnitude of these distortions varies across body parts inversely with respect to the tactile sensitivity of that body part - and consequently its representation in the primary somatosensory cortex (see Figure 1). Thus, the length of less tactilely sensitive body parts, such as the torso, were overestimated more than more sensitive body parts, such as the arm (Linkenauger et al., 2014). Importantly, when using a hand-length wooden dowel (or a drawing of their hand) as a metric to estimate their body parts, individuals overestimate their body proportions slightly but to a drastically reduced magnitude, and the overestimation did not systematically differ across different body parts. By contrast, when a non-sensitive body part was used as a metric (i.e., the forearm), individuals underestimate, rather than overestimating their body parts, with a gradient in which less sensitive body parts were underestimated less.

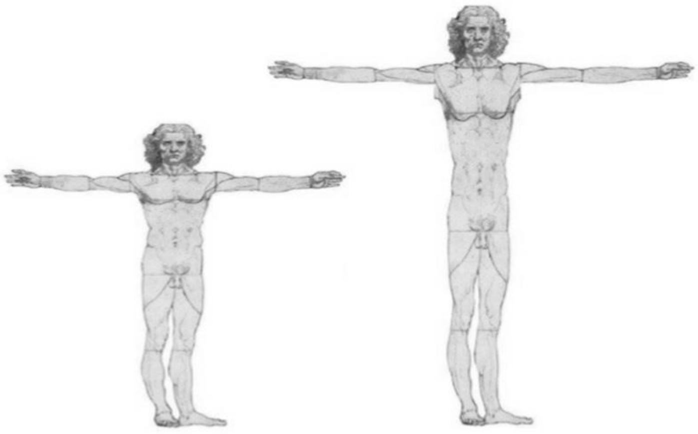

Figure 1. Scaled illustrations of individuals' perceptions of their body proportions (right) and their actual body proportions (left).

The receptive fields of neurons in the primary somatosensory cortex representing sensitive skin surfaces, such as the hand or the foot, are smaller and denser than those representing less sensitive skin surfaces, such as the torso (Penfield & Rasmussen, 1950). This leads to a larger representation in the primary somatosensory cortex for more sensitive body parts (Penfield & Boldrey, 1937). This differential distribution results in objects feeling larger on more sensitive body parts, because the object stimulates more somatosensory receptive fields than on less sensitive body parts, an effect popularly referred to as *Weber's illusion* (Weber, 1834/1996, see next section). Given that the estimation of body parts' lengths were distorted in inverse relation to the size of the cortical somatosensory representation, Linkenauger and colleagues (2014) suggest that a compensatory mechanism is responsible to produce a reasonable degree of tactile size constancy across different body parts, thereby possibly counteracting Weber's illusion. The fact that these distortions were only present when comparing body parts relative to one another, and drastically reduced when comparing body parts with an object (e.g., dowel), suggest that this effect arises from systematic asymmetries in the representation of different parts of the body. Several studies support the relation between perceived size of a body part and its cortical somatosensory representation. For instance, decreases in a body part's sensitivity via anaesthesia leads to increases in the perception of its size (Gandevia & Phegan, 1999). Furthermore, chronic pain in a given body part typically reduces the size of the cortical somatosensory representation of that body part and increases the perceived size of the body part (Gandevia & Phegan, 1999; Moseley, 2005).

Nonetheless, recent findings have shown that these distortions are also present when individuals use an experimenter's hand to estimate the experimenter's body dimension (Linkenauger, Kirby, McCulloch & Longo, in preparation), which casts some doubt on the reverse distortion hypothesis. Additionally, these distortions appear when viewing the bodies of people in pictures, so it is possible that they are driven by an internal model of the body used to organize the visual information specific to the human bodies. However, these two explanations are not mutually exclusive in that this internal model could possibly have been shaped by the need for reverse distortion. Future research will aid in coming to a more definitive answer to the origin of these distortions.

Overall, the evidence from the studies we just described suggests that vision influences the way we represent our bodies. Moreover, even with sufficient visual information specifying our body proportions, large distortions are nevertheless present. As we will see in the next section, these distortions arise most like from the influences of the tactile modality.

Touch, proprioception and the body

Touch and the body are intimately related given that the primary receptor surface for touch – the skin – is physically co-extensive with the surface of the body. Indeed, touch along with related senses such as nociception (the focus on the last section) are commonly termed the “bodily senses”, highlighting their profound and intimate link. Investigations of the link between touch and the body have often focused on the perception of tactile size or distance. This is because judging how far apart two touched locations on the skin are does not appear to be specified by any afferent signal, but appears to require referencing to a representation of body size and shape, which Longo and colleagues (Longo et al., 2010) referred to as the “body model”. The idea of the body model arose from the observation that nothing in the flow of raw afferent signals provides direct information on the exact metric spatial relations among stimuli. For example, if afferent signals indicate that touches occurred on either side of the hand, determining the distance between the touches requires referencing to a representation of hand size. Indeed, several types of manipulation of high-level representation of body size and shape have been found to produce systematic modulation of tactile size perception. Taylor-Clarke and colleagues (Taylor-Clarke, Jacobsen, & Haggard, 2004), for example, used a visual distortion procedure to give participants prolonged visual experience of their forearm magnified and hand minified. After this exposure, perceived tactile distances were expanded on the forearm and compressed on the hand compared to baseline. Analogous effects have been found following other sorts of bodily illusions, such as those induced by proprioceptive-tactile illusions (de Vignemont, Ehrsson, & Haggard, 2005), auditory-tactile illusions (Tajadura-Jiménez et al., 2012), the rubber hand illusion (Bruno & Bertamini, 2010), and tool use (Canzoneri et al., 2013; Miller, Longo, & Saygin, 2014). Even passive, non-informative vision of the stimulated limb modulates perceived tactile distance (Longo & Sadibolova, 2013). Moreover, perceived tactile distances are expanded across body-part boundaries (de Vignemont, Majid, Jola, & Haggard, 2009; Le Cornu Knight, Longo, & Bremner, 2014), suggesting that the high-level segmentation of the body into discrete parts also influences tactile perception.

In contrast to the research just presented, other work has shown that tactile distance perception is not fully determined by high-level body representations, but is also shaped by quite low-level aspects of somatosensory organization. As mentioned above, Ernst Weber (1834/1996), experimenting on himself, discovered the curious illusion which now bears his name. Moving the two points of a compass across his skin, he found that the distance between them felt larger when applied to a sensitive skin surface (e.g., the palm of the hand) than when applied to a less sensitive surface (e.g., the forearm). Weber's Illusion has been confirmed and extended by subsequent research, which has shown a systematic relation between the tactile spatial sensitivity of skin surfaces and the perceived distance between touched points (Cholewiak, 1999; Taylor-Clarke et al., 2004). One natural interpretation of this effect is that the metric structure of tactile space preserves the characteristic distortions of early maps of the skin in somatosensory cortex, the so-called "Penfield homunculus" (Penfield & Boldrey, 1937). Critically, however, the magnitude of Weber's illusion is dramatically smaller than would be expected if tactile distances were perceived in direct proportion to the cortical magnification factors of different skin surfaces. This suggests the operation of a process of tactile size constancy which (partially) corrects for these distortions, a process possibly related to the higher-level body referencing described in the preceding paragraph. This poses a parallel between the distortions observed in vision and touch, with a putative common origin and mediated by similar processes of size constancy.

In its classic form described above, Weber's illusion compares the perceived size of tactile distances presented to different skin surfaces. In this sense, it investigates the relative size of each part. An analogous logic, however, can be used to investigate the represented shape of individual skin surfaces by comparing the perceived size of tactile distances in different orientations on a single skin surface. Longo and Haggard (2011), for example, found that tactile distances oriented across the width of the hand dorsum were perceived as approximately 40% larger than identical distances rotated 90˚ along the length of the hand. This effect is dramatically reduced on the palmar surface of the hand. Intriguingly, this difference between skin surfaces mirrors differences in the shape of receptive fields of neurons in somatosensory cortex, which are elongated along the proximo-distal axis on hairy skin (Alloway, Rosenthal, & Burton, 1989) but more circular on glabrous skin (DiCarlo, Johnson, & Hsiao, 1998). This suggests that the geometry of receptive fields in somatotopic cortical maps may play a fundamental role in shaping the structure of tactile space. Additional studies have revealed similar anisotropies on other skin surfaces, including the forearm (Green, 1982; Le Cornu Knight et al., 2014), the face (Longo, Ghosh, & Yahya, 2015), and the leg (Green, 1982). This suggests that distortion may be a general feature of the representation of tactile space.

Interestingly, similar distortions have been found in proprioception. In analogy to tactile distance perception, the absolute location of body parts in space also require the referral of a “body model”, as proprioceptive information is unable to signal the length of limb segments (Longo et al., 2010; Proske & Gandevia, 2012). As for touch, the body model mediating proprioceptive localisation seems to be systematically distorted (Longo, 2015; Longo & Haggard, 2010). Longo and Haggard (2010) asked participants to rest their hand still and point with the other hand to the locations of fingertips and knuckles, while their hand was occluded from view. The results revealed a distorted map with the fingers shorter than their actual size and the hand broader than it really was, similar to the distortions found for touch. Critically, these distortions are observed even for congenital phantom limbs (Longo et al., 2012). In contrast to these distortions, explicit judgements of hand shape using a template-matching task were accurate, suggesting that the body image and the implicit body representation underlying human position sense are two different representations. Furthermore, additional distortions related to proprioceptive signals have been found when subjects are asked to point to different parts of their hidden arm (Gross, Webb, & Melzack, 1974). Participant responses show that the resting arm is systematically perceived to be closer to the midline of the body on the right-left dimension, and closer to the body on the near-far dimension than it really is (Gross, Webb, & Melzack, 1974; but see Rincon-Gonzalez, Buneo, & Helms Tillery, 2011).

Finally, the influence of proprioception on body representation is evident when using muscle vibration to generate proprioceptive misinformation about limb position. For example, vibrating the biceps tendon produces the illusion of elbow extension, while vibrating the triceps tendon produces the illusion of elbow flexion. Lackner (1988), for instance, was able to generate in a matter of seconds systematic perceptual distortions of the body and changes in the apparent orientation of the body, after applying vibration to different muscles. A classic example of these distortions is the Pinocchio illusion. By having participants grasping their nose while vibrating the biceps or triceps tendons of the grasping arm, Lackner produced the illusion that the nose was either lengthening or coming inwards the head, depending on which muscle was stimulated (Lackner, 1988; see also de Vignemont, Ehrsson, & Haggard, 2005; Ehrsson et al., 2005).

In this section we have discussed the role of body representations in providing metric structure to touch and position sense. In both cases, these representations appear to be highly distorted, at least in the case of the hands, with overrepresentation of hand width compared to length. Intriguingly, these perceptual distortions mirror distortions in the geometry of tactile receptive fields in somatosensory cortex. This suggests bilateral causal influences between higher-level representations of the body and lower-level sensory representations.

Vestibular contributions to body representation

The vestibular sense, similar to touch, is intimately related to the inner experience of having a body. Three orthogonal semi-circular canals detect rotational movements of the head in the three-dimensional space (i.e., pitch, yaw and roll), and two otolith organs (utricle and saccule) sense translational acceleration, including the gravitational vertical. Information from these vestibular peripheral organs is integrated with several other classes of signals about the body, such as vision, touch, and proprioception. This convergence seems to reflect a fundamental mechanism for maintaining the perception of the body relative to the external environment (Berthoz, 1996).

Interestingly, no unimodal vestibular cortex has been identified in the mammalian brain. For instance, several classical somatosensory areas also receive vestibular inputs. The somatosensory cortices respond to both vestibular and somatosensory signals (Bottini et al., 1995; Lopez & Blanke, 2011; Lopez, Blanke, & Mast, 2012; zu Eulenburg, Baumgärtner, Treede, & Dieterich, 2013), and are thus good candidates for mediating interactions between the vestibular and somatosensory systems. For example, artificial vestibular stimulation modulates psychophysical thresholds for both touch and pain (Ferrè, Bottini, Iannetti, & Haggard, 2013; Ferrè, Day, Bottini, & Haggard, 2013; Ferrè, Sedda, Gandola, & Bottini, 2011), and enhances specific waves of somatosensory-evoked potentials generated in the right opercular region (Ferrè, Bottini, & Haggard, 2012). Clinical observations also lend support to the notion of cross-modal interactions between the vestibular and somatosensory systems (Kerkhoff et al., 2011; Schmidt et al., 2013; Vallar, Bottini, Rusconi, & Sterzi, 1993; Vallar, Sterzi, Bottini, Cappa, & Rusconi, 1990).

Vestibular signals also contribute to other, more cognitive, aspects of bodily representation. For instance, vestibular inputs are important for the perception of the size and shape of body parts (Lopez et al., 2012). As we have described in the previous section, no peripheral receptors are directly informative about such features, and therefore this knowledge is plausibly linked to the distorted body model proposed by Longo and colleagues (2010). At least for the hand, these distortions included a radial–ulnar gradient of magnification of the digits and shrinkage toward the proximo-distal axis. Interestingly, vestibular stimulation appears to increase the perceived length and width of the hand compared to sham stimulation (Lopez, Schreyer, Preuss, & Mast, 2012; but see also Ferrè, Vagnoni, & Haggard, 2013), suggesting it forms an input to such internal models of the body.

The most convincing evidence for vestibular contributions to body representation comes from neuropsychological patients. Indeed, case studies of individuals with right hemisphere damage have found temporary remissions of somatoparaphrenia (i.e. denial of ownership of contralesional body parts, Vallar & Ronchi, 2009) following artificial vestibular stimulation (Bisiach, Rusconi, & Vallar, 1991; Rode et al., 1992). These reports suggest a vestibular contribution to body ownership, such as the feeling that one's body belongs to oneself, over and above any particular bodily sensation (Metzinger, 2003). This hypothesis has been recently explored in healthy participants using the rubber hand illusion (Botvinick & Cohen, 1998). Combining the rubber hand illusion with artificial vestibular stimulation revealed a vestibular-induced modulation of the strength of the illusion (Ferrè, Berlot, & Haggard, 2015). Indeed, the vestibular stimulation polarity that predominantly activates the vestibular projections in the right hemisphere produced a smaller proprioceptive shift toward the rubber hand compared with the opposite polarity (Ferrè et al., 2015). The right hemisphere vestibular network therefore, increases the salience of intrinsic somatosensory and proprioceptive signals about hand position, and decreases the salience of visual information responsible for visual capture during the rubber hand illusion. However, Lopez and colleagues (Lopez, Lenggenhager, & Blanke, 2010) found a vestibular induced enhancement of the RHI as measured by questionnaires using the same stimulation polarity, but no reliable effects on proprioceptive drift. Nonetheless, it is important to note that the experimental setup and vestibular stimulation procedure used in these studies differed in several aspects, rendering any direct comparison difficult. First, the duration of vestibular stimulation was much longer in Lopez et al. (2010) than Ferrè et al. (2015). Second, Lopez et al. (2010) used a blocked design, whereas Ferrè et al. (2015) used a randomised, event-related design. Finally, it is notable that proprioceptive drift (Ferrè et al., 2015) and questionnaires (Lopez et al., 2010) are two different and independent aspects of the rubber hand illusion (Rohde, Di Luca, & Ernst, 2011).

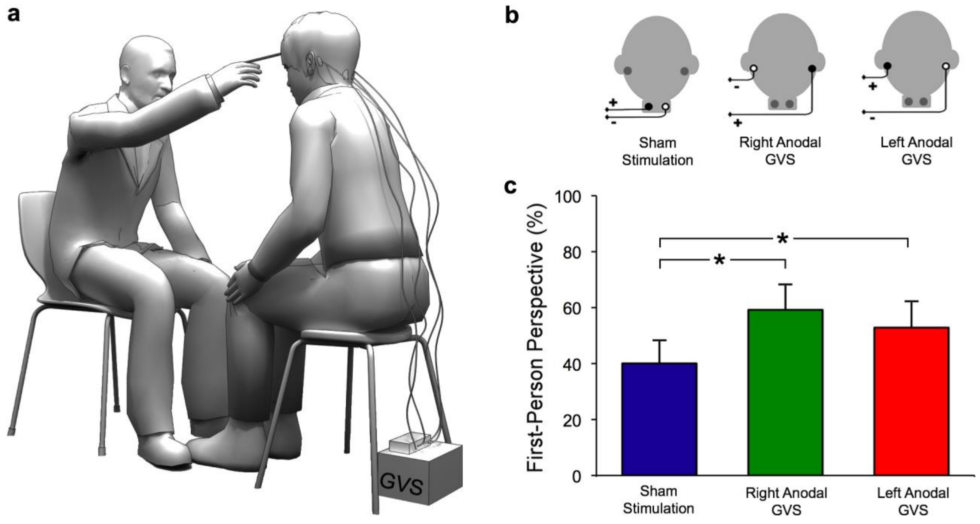

Figure 2. Effect of vestibular stimulation (GVS) on perspective-taking. **(a)** An ambiguous letter (b, d, p, or q) was traced by the experimenter on the participant's forehead. The task was to name the letter. **(b)** GVS (right-anodal/left-cathodal) or sham stimulation was applied on different blocks. **(c)** Vestibular stimulation increased the probability that ambiguous letters were interpreted with an internal first-person perspective. Adapted with permission from Ferrè et al., 2014.

A coherent representation of the body is more than having ownership over single body parts. The feeling of "mineness", i.e., the feeling that one's body belongs to oneself, implies a spatial unity between the self and the physical body. Indeed, a first-person perspective tags almost all our bodily experiences. This can be seen as a proxy of the spatial unity between the self and the physical body. Recently, Ferrè and colleagues (2014) investigated whether vestibular signals influence the perspective people take (first-person perspective vs third-person perspective) in interpreting ambiguous tactile stimuli (Natsoulas & Dubanoski, 1964). Artificial vestibular stimulation was delivered while an experimenter drew ambiguous letters (b, d, p, q) on the participant's forehead, a well-established task of implicit perspective-taking (Figure 2a-b). These letters can be perceived either from the internal first-person perspective (e.g. letter 'b' perceives as letter 'd') or from an external third-person perspective (e.g. letter 'b' perceived as letter 'b'). Vestibular stimulation increased the likelihood that ambiguous letters were interpreted with an internal first-person perspective (Figure 2c).

The vestibular system provides fundamental information about the position and motion of the body, relative to the external environment. However, the studies presented in the present chapter suggest that vestibular signals are not only an input for motor control and postural responses, but also a distinct source of information about one's own body.

Auditory contributions to body representation

The link between audition and body representations has received far less attention than that of other modalities. Thus, the extent to which the auditory system contributes to constructing body representations remains largely unexplored. Nevertheless, there is some evidence that sounds generated when interacting with objects and surfaces can change body awareness and impact on the perception of the body as a physical object.

Some studies have demonstrated that sounds coming from external sources or emanating from one's body have an effect on the overall body awareness. For instance, Murray and colleagues (2000) conducted a study in which earplugs were used to induce hearing loss. Participants in this study reported a sensation of detachment from the surroundings and also altered awareness of their movements and of their own bodily sounds, such as the sounds produced when breathing, eating or by their blood-flow (Murray, Arnold, & Thornton, 2000). Other studies have shown that hearing pre-recorded heartbeat sounds influences participants' beliefs about their own heart rate (Phillips, Jones, Rieger, & Snell, 1999) and eventually elicits changes in participants' own heart rate and emotional state (Tajadura-Jiménez, Väljamäe, & Västfjäll, 2008). In virtual reality contexts, sounds representing one's body moving (i.e., a sonic self-avatar) are known to enhance the sensation of self-motion and of presence in the virtual environment (Väljamäe, Tajadura Jimenez, Larsson, Västfjäll, & Kleiner, 2008). Further, in sports and rehabilitation contexts, sound feedback of body movements is sometimes provided to enhance body and movement awareness (Cesarini, Hermann, & Ungerechts, 2014; Großhauser, Bläsing, Spieth, & Hermann, 2012; Sigrist, Rauter, Riener, & Wolf, 2013; Singh et al., 2014).

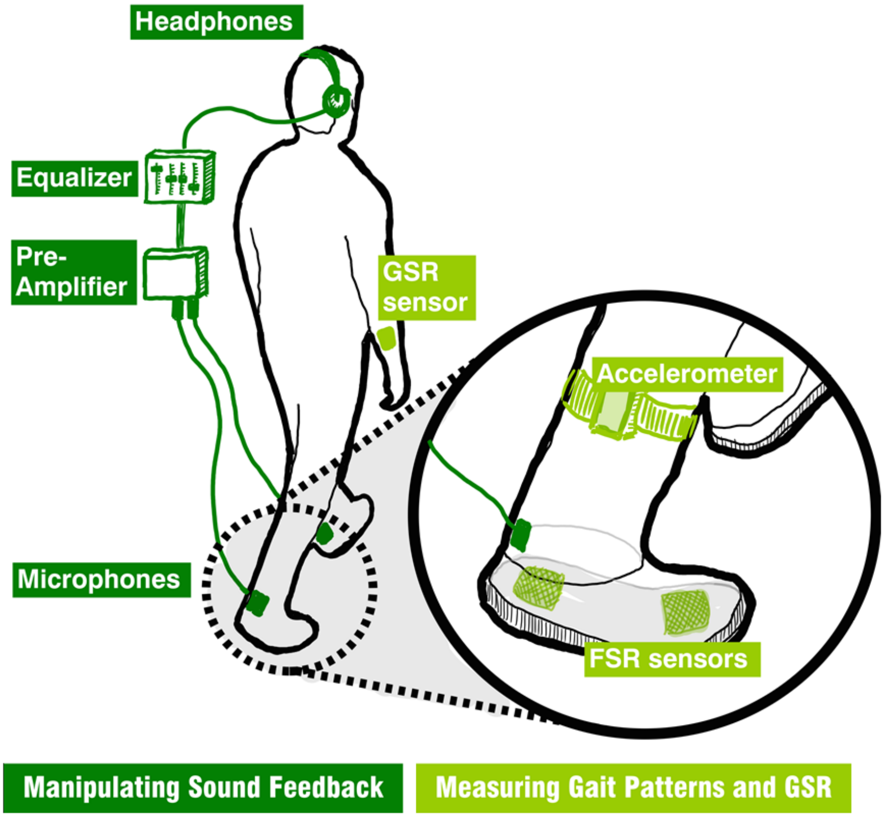

Figure 3. Manipulating sound-feedback and sensing gait and emotion (GSR: Galvanic Skin Response; FSR: Force Sensitive Resistor). Short adaptation periods to altered walking sounds led to lower perceived body weight, to the adoption of gait patterns typical of lighter bodies and to an enhanced emotional state. Adapted with permission from (Tajadura-Jiménez, Basia, et al., 2015).

Listening to action related sounds can affect action planning and execution. Indeed, neuroscience research has shown that listening to sounds that were produced when performing certain actions activates the same brain areas that would have been recruited when preparing to perform these actions (Aglioti & Pazzaglia, 2010; Pazzaglia, Smania, Corato, & Aglioti, 2008). Other studies have shown that real-time alteration of the sounds produced when performing actions results in an adjustment of motor behavior. For instance, delaying walking sounds or altering cues that are related to the strength applied when tapping a surface, results in the adjustment, respectively, of the walking (Menzer et al., 2010) and tapping behavior (Tajadura-Jiménez, Furfaro, Bianchi-Berthouze, & Bevilacqua, 2015).

Sound can also have an effect on the perceived body as a physical object. A few studies have shown effects of sound in perceived body material properties. For instance, altering the spectra and/or amplitude of the sounds produced when rubbing two hands together changes the perceived smoothness and dryness of the skin (Jousmäki & Hari, 1998). Similarly, hearing the sound produced when an object hits marble in synchrony with the feeling of an object hitting one’s own hand, makes this hand to be felt stiffer and heavier (Senna, Maravita, Bolognini, & Parise, 2014). People also feel as if their body were made of metallic parts (“robotized”) when they receive sound and vibro-tactile stimuli, built from recordings of a real robot actuation, simultaneously with their movements (Kurihara, Hachisu, Kuchenbecker, & Kajimoto, 2013). These studies used spatialized sounds in order to give the impression that the sounds were actually coming from one's own body (i.e., either originating from the stimulated body part, as in Kurihara et al., 2013, or manipulated so that they were perceived as if originating from the same position of the manipulated body part, as in Senna et al., 2014). Nonetheless, a few studies have shown that altering the spatial location of action related sounds with respect to the manipulated body part can, for instance, lead to alterations in tactile distance and in the represented body dimensions, if the spatial manipulations are kept within certain limits, so that the sounds are still perceived as coming from one's body (Tajadura-Jiménez et al., 2012; Tajadura-Jiménez, Tsakiris, Marquardt, & Bianchi-Berthouze, 2015). For instance, altering the spatial location of sounds produced when one's own hand taps a surface, with the resulting sounds originating at a double distance at which one is actually tapping, can lead to changes in the represented length of the arm. These changes were measured by looking at variations in the perception of tactile distances on the tapping arm and variations in subjective feelings of arm length (Tajadura-Jiménez et al., 2012, 2015). Similarly, altering the frequency spectra of sounds produced when walking, so that the resulting sounds are consistent with those produced by either a lighter or heavier body, can result in changes in the representation of one's own entire body size and weight (Tajadura-Jiménez, Basia, et al., 2015). Changes in the walking sounds were also connected to changes in walking behavior and emotional state (see also Tonetto, Klanovicz, & Spence, 2014).

Overall, these studies provide evidence that sounds can impact on body awareness, body movement and body representations. The studies reporting auditory-driven changes in body representations showed that those changes were connected to effects in tactile perception, motor behaviour and emotional state. These results suggest that the way we represent our body is supramodal and that it has profound implications in the way we perform actions and in emotional state.

Neuropsychological evidence about multisensory control of pain

Among the sensory input we can experience, pain is surely the most unpleasant. However, pain is also fundamental for our survival, given that its occurrence is usually linked to a current or potential damage to the body. Pain responses start to the mere knowledge of a threatening stimulus approaching the body (anticipation, Ploghaus et al., 1999; expectation, Brown, Seymour, Boyle, El-Deredy, & Jones, 2008) and trigger defensive reactions on direct (Graziano & Cooke, 2006) and indirect pain experience, for instance, when observing the pain of others (Avenanti, Minio-Paluello, Minio Paluello, Bufalari, & Aglioti, 2006). To this aim, pain is strictly linked to the representation of the body, with dedicated neural pathways for sensory analysis, reflex reactions and cognitive appraisal of the painful experience (Price, 2000). Indeed, it has been recently proposed that pain experience may have critically contributed to shaping sensorimotor representation of the body and its surrounding space for defensive purposes (Haggard, Iannetti, & Longo, 2013).

The interaction between body representation and pain is bi-directional. On one side, the integration of pain experience with the ongoing representation of our body is critical to localize the source of a painful stimulus and react to it. On the other side, pain conditions, and in particular chronic pain, can affect the way in which we experience our body, leading to sensorimotor disturbances. For example, complex regional pain syndrome (CRPS-1) may lead to motor (Galer, Butler, & Jensen, 1995) or proprioceptive (Lewis et al., 2010) impairments, following a “neglect-like” pattern. This is reminiscent of the behaviour of patients who fail to attend to the contralesional side of their body or space, following brain damage (Vallar & Maravita, 2009). Furthermore, clinical conditions consisting of chronic pain symptoms, even those as common as low back pain, can deeply affect the general feeling about the physical integrity of the body and its motor potentials, triggering deleterious avoidance behaviours that strongly limit the patients’ daily life activities and progressively deepen their clinical picture (Jensen, Turner, & Romano, 2001).

In the present section, we will consider two aspects of the influence of body representation on pain experience that have recently attracted the attention of researchers: first, the modulatory interaction between vision of the body and pain; second, the necessity of an intact sense of body ownership for the processing of pain stimuli.

The first issue is grounded on the evidence that pain is subject to significant multisensory integration, similarly to other sensory modalities. On an early level, concurrent somatosensory input are known to reduce pain sensations as famously theorized, for example, by the gate-control theory (Melzack & Wall, 1965). Proprioception has also shown to affect pain processing, with the reduction of pain sensation on crossing the arms (Gallace, Torta, Moseley, & Iannetti, 2011; Valentini, Koch, & Aglioti, 2015), in line with the notion of an interplay between different mappings of somatic sensations in somatotopic coordinates and in the external egocentric space (Yamamoto & Kitazawa, 2001). Also touch and temperature have shown interesting effects on pain perception, as demonstrated through the thermal grill illusion (Craig & Bushnell, 1994; Kammers, de Vignemont, & Haggard, 2010).

Above all, vision has shown to exert a strong influence on pain experience. Early studies in neurological patients have assessed the reduction of chronic pain following amputation or complex regional pain syndrome (McCabe et al., 2003; Ramachandran & Altschuler, 2009), by looking at a parasagittal mirror where the reflected image of the intact limb mimics the affected limb beyond the mirror (the so-called Mirror Box setting). Further evidence gathered from neurologically intact individuals have shown similar reductions of experimentally-induced acute pain by vision of a body part (Longo, Betti, Aglioti, & Haggard, 2009). The close relationship between visual analysis of body parts and pain processing has been recently quantified through functional imaging work showing a close relationship between posterior areas devoted to the visual representation of the body and elements of the pain network, while looking at body parts targeted by painful laser stimulations (Longo, Iannetti, Mancini, Driver, & Haggard, 2012).

Intriguingly, as in the case of touch (Kennett et al., 2001) and movement (Bernardi et al., 2013; Marino, Stucchi, Nava, Haggard, & Maravita, 2010), the distortion of visual feedback about the body can modulate pain perception. A reduction of pain can be obtained by providing visual feedback of a reduced image of the affected body part, in patients suffering from chronic pain, or a visually reduced reflection of the intact limb, in patients suffering from phantom limb pain (Moseley, Parsons, & Spence, 2008; Ramachandran, Brang, & McGeoch, 2009). In these situations, pain feelings decrease following visual reduction and increase following visual magnification of the affected body part. By contrast, in neurologically intact humans, visual body magnification reduces perceived intensity as well as physiological responses to pain (Mancini, Longo, Kammers, & Haggard, 2011; Romano & Maravita, 2014). The work by Romano and Maravita (2014) explored the dynamics of the analgesic response induced by visual magnification of the body using skin conductance, showing that reduced arousal and perceived intensity of pain on stimulus contact were preceded by increased arousal responses when the threatening stimulus approached the body. In other words, more intense anticipatory responses were followed by reduced somatic pain responses, as consequence of visual body magnification. Thus, opposite effects of visual magnification have been found in chronic or acute pain conditions, with increased and reduced responses to pain, respectively. This could be due to the different correlates of chronic and acute pain in the brain, as well as the plastic changes that are likely induced by chronic pain conditions, both in the processing of sensory inputs and in body representations. Neural changes following chronic pain are known to occur at all levels in the central nervous system. In the afferent nociceptive and somatosensory pathways, deep synaptic and molecular membrane reorganization processes occur following either chronic neuropathic pain or deafferentation (Gold & Gebhart, 2010). In the cortex a large amount of plasticity occurs following deafferentation. The amount of such plasticity, in particular the shift of the hand area in the body representation in the primary somatosensory cortex, has been linked to the amount of phantom limb pain, calling for a “maladaptive plasticity” in such patients (Flor et al., 1995; Flor, Nikolajsen, & Staehelin Jensen, 2006; Foell, Bekrater-Bodmann, Diers, & Flor, 2014; Lotze, Flor, Grodd, Larbig, & Birbaumer, 2001; though see Makin, Scholz, Henderson Slater, Johansen-Berg, & Tracey, 2015, for recent contrasting evidence). This evidence suggests a strict link between body representation (or, better, disruption of body representation) and the sensory experience of pain. Furthermore, it has been proposed that therapeutic strategies based on electrical stimulation of the brain, may reduce pain by targeting the neural maladaptive sensory reorganization (Bolognini et al., 2015; Bolognini, Olgiati, Maravita, Ferraro, & Fregni, 2013).

Regarding the second aspect of interest in this section, i.e., the necessity of an intact sense of body ownership for the processing of pain stimuli, recent findings have uncovered the role of body awareness in maintaining intact responses to nociceptive stimuli. In particular, the interaction with threatening stimuli in peripersonal space, that typically produces alerting anticipatory responses, has shown to be disrupted by defective bodily awareness following brain damage. In a group of patients affected by somatoparaphrenia, Romano and colleagues (Romano, Gandola, Bottini, & Maravita, 2014) have shown an absence of anticipatory electrodermic response to the vision of approaching threatening stimuli, as compared to the non-affected hand or to the contralesional hand of patients affected by anosognosia (i.e., denial of sensory deficit but not of body ownership) or hemiplegia, but without any delusion of body ownership. Such findings suggest that intact sense of body ownership is necessary in order to evaluate the impact of an incoming threat and produce a preparatory response towards it. Furthermore, they highlight that somatoparaphrenic patients are not only impaired in their inner representation of the body (Vallar & Ronchi, 2009), but also in their possibility of monitoring their peripersonal space for incoming threats. This underlines the strong link between the representation of the body and the peripersonal space (Macaluso & Maravita, 2010; Maravita, Spence, & Driver, 2003), where the potentially negative and threatening value of visual stimuli approaching the body is taken into account, in order to trigger defensive behaviors (Graziano & Cooke, 2006; Haggard et al., 2013). A logically related finding linking body awareness and pain processing is the recent discovery that, when the sense of body ownership is partially transferred to an avatar, following a Full Body Illusion paradigm, the response to a painful stimulus is reduced (Romano, Pfeiffer, Maravita, & Blanke, 2014).

In summary, the experimental evidence briefly reviewed above calls for a strict relationship between pain processing and vision, and adds to broader evidence that the processing of pain is integrated with that of other sensory modalities in shaping peripersonal space (Haggard et al., 2013). On one side, it shows that vision, altering the online representation of the body, affects pain. On the other, it shows that disrupted body representation, as observed in somatoparaphrenic patients, affects pain processing, suggesting, again, a strict link between body knowledge and the monitoring of peripersonal space for pain processing (Romano, Gandola, et al., 2014).

Discussion

In this review we described some of the most recent evidence of the contribution of each sensory modality to the creation of coherent representations of the body, focusing on the topics discussed in the symposium on Multimodal Contributions to Body Representation (15th International Multisensory Research Forum, 2015, Pisa, Italy). We have seen how different sensory modalities and their interactions can contribute to form body representations and influence bodily-related experiences. In this respect, we have shown that the perceived visual proportion of the body is distorted with an overestimation of the dimension of each body part. These distortions are inversely related to tactile sensitivity of the skin area, which has led researchers to interpret this disparity as a compensatory mechanism, possibly necessary to achieve a good degree of tactile size constancy across different body parts. Similarly, analogous distortions emerge also when the sensory input is tactile. For instance, we have shown that tactile distances oriented across the width of the hand dorsum are perceived larger than identical distances presented along the length of the hand and that this effect is dramatically reduced on the palmar surface of the hand. Notably, perceptual differences between the dorsum and the palm mirror the shape of receptive fields in the primary somatosensory cortex, suggesting a critical role of the geometry of the tactile receptive fields in shaping the structure of the tactile space. Therefore, perception of the tactile distance on the body is not fully determined by high-level body representations, but is also shaped by quite low-level aspects of somatosensory organization. With regard to the vestibular system, it seems to provide a direct input to these internal models of the body, with the ability to modify intrinsic properties of it, such as the perception of its size and shape. Intriguingly, some studies have highlighted a vestibular contribution to critical aspects of body awareness, such as the feeling that one's body belongs to oneself or the perspective we take in interpreting ambiguous bodily signals. We have also demonstrated that sounds coming both from external sources and from one’s own body have consequences on the way we perceive and represent our bodies. In particular, we have highlighted changes in body awareness, in the perception of body size and length and even in the way we plan and execute actions. Even more striking, altering some components of the sounds produced when performing actions modify the perceived material we are made of. Finally, we have highlighted the modulatory effect that other sensory modalities have on pain perception and the necessity of an intact sense of body ownership for a correct processing of pain stimuli. For instance, we have shown that a magnified vision of a body part can induce analgesic effects in healthy subjects, while exacerbates pain in patients suffering from chronic pain and amputees with phantom limb pain. Overall, we have shown that the different sensory modalities, mostly in combination, play a fundamental role in the way we construct the variety of multisensory representations that we use to perceive, feel or remember our bodies, and that ultimately are critical to interact with the environment.

We have discussed each modality in its own section, focusing on one modality at a time. Such a *divide-and-conquer* approach is useful experimentally, but highly implausible in reality. Indeed, when perceiving the body, it is nearly impossible to obtain sensory information from a single modality in isolation. This issue becomes even more complex when studying the tactile modality, as somatosensory and proprioceptive systems provide simultaneously constant information about the body, and “turning off” input from these sensory systems is virtually impossible. The results of the studies reviewed here, therefore, produce an image of the representation of the body as a multisensory concept with the different senses interacting to contribute to the formation of body representations.

Despite the large amount of evidence reported in this review, we believe that several key questions remain unanswered. Among others, a relevant question is the weight or impact each modality has on different body representations. Namely, whether there is a sense that is primarily used to determine the way in which we perceive our body. Vision, which is considered to be the dominant sense in many aspects of cognition and perception, might be expected to be similarly dominant in the representation of our body. However, in the case of body representations, touch, nociception, and proprioception might also play crucial roles, given their physically co-extent with the surface of the body. The vestibular sense, mediating position and body motion, and audition, with its intimate relation with action, are also plausible suspects. A related question is whether in particular situations, such as in visually impaired or deaf individuals, the intact sensory modalities are able to produce complete and holistic bodily experiences. Assuming that this is the case, a straightforward question relates to the compensatory mechanisms that allow people with sensory deficits to overcome these impairments (see Nava et al., 2014; Petkova et al., 2012). Further, in future studies it would be interesting to explore the development of multisensory integration (Burr & Gori, 2012) used to achieve appropriate body representations. Indeed, a growing body of literature in the topic have found that children and even newborns are sensitive to body-related, synchronous visuo-tactile stimuli (Bremner, Mareschal, Lloyd-Fox, & Spence, 2008), suggesting that key processes underlying body perception are present at birth (Filippetti, Johnson, Lloyd-Fox, Dragovic, & Farroni, 2013; Filippetti, Orioli, Johnson, & Farroni, 2015; Marshall & Meltzoff, 2011). Finally, it is important to highlight that action is often a missing concept in the body representation literature. It is an implicit statement that the way we represent our body has profound implications in the way we perform appropriate actions. However, although considered (Cardinali et al., 2009), little attention has been given to the relation between body representations and actual movement or goal directed actions. For instance, some of the distortions reported in the tactile and visual sections of this review might be functional to action, or similarly, the high malleability of body representations might be strictly linked to the fact that we can perform appropriate actions.

Taken together, we have described ways in which vision, touch, audition, pain and the vestibular system shape body representations during the daily multisensory experiences and how these representations affect the way we perceive the world through the senses. Further experiments investigating the relationship between action execution and body representation will certainly be an important direction for future research. This may help to unfold, if it exists, a functional reason for this peculiar way in which we represent our body.

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