

# Multimodal Contributions to Body Representation

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Pages: 33; Figures: 2; Abstract: 183/250; Words=

Keywords: MULTISENSORY INTEGRATION, BODY REPRESENTATIONS, VISION, TOUCH, AUDITION, PAIN, VESTIBULAR SYSTEM

Running head:

## **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.

## 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 inevitably 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 worlds, we are also exposed to visual and auditory signals related to our body (Gibson, 1966). All these inputs are combined to construct the large variety of body representations that we have (Longo et al., 2010). These include those related to what we perceive our body as being like, but also those related to how we remember or believe the body is (de Vignemont, 2010; Schwoebel & Coslett, 2005). Importantly, this process is not unidirectional, and the way we represent our body has also a reciprocal implication in the way we process and locate bodily sensations (e.g., Keizer et al., 2011; Paillard, 1999).

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” (RHI, 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 (e.g., 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 (e.g., 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).

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 in the topic. We will start by showing how experiencing pain can affect the representation of the body and in which way the visual modality can produce beneficial analgesic effects. We will continue 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 tactile constancy despite differences in tactile receptive field 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. Finally, we will discuss how sounds that accompany almost every of our bodily movements are used to form body representations. The review will end with a concluding remark of the current state of the art of research on sensory contributions to body representation, ending with proposals for future investigations.

### **Neuropsychological evidence about multisensory control of pain**

Among the several instances demonstrating multisensory integration in the human brain, pain has recently come to the attention of the scientific community for both its heuristic implications and clinical applications. The possibility that pain sensations can be strongly modulated by both sensory and non-sensory manipulations is rooted in the multifactorial nature of pain processing. A number of cortical structures contribute to pain, ensuring a rich and variable experience, from early arousal reactions, to somatotopic pain localization in primary sensory areas (Mancini, Haggard, Iannetti, Longo, & Sereno, 2012), to posterior parietal, cingulate, insular, and prefrontal cortex, all serving different aspects of pain experience (e.g., Price, 2000; Rainville, Carrier, Hofbauer, Bushnell, & Duncan, 1999). A putative “pain network” emerges from the literature, the role of which may not be limited to the processing of pain, but may be more generally devoted to the processing of salient events (Legrain, Iannetti, Plaghki, & Mouraux, 2011).

The knowledge of such complex circuits helps understanding how pain experience emerges. In particular in chronic pathological conditions the central nervous system can undergo maladaptive plasticity at multiple levels, such as in the case of deafferentation (Flor, Nikolajsen, & Staehelin Jensen, 2006; Karl, Birbaumer, Lutzenberger, Cohen, & Flor, 2001). Similarly, it can help understand how pain can be successfully modulated by external intervention that go beyond the classical pharmacological interventions, from brain stimulation (e.g., for the treatment of headache, Brighina, Cosentino, & Fierro, 2013) or phantom limb pain (Bolognini et al., 2015; Bolognini, Olgiati, Maravita, Ferraro, & Fregni, 2013), to hypnosis (Elkins, Jensen, & Patterson, 2007), meditation (Bushnell, Ceko, & Low, 2013; Zeidan et al., 2011), or psychosocial approaches to the treatment of chronic pain conditions, such as low back pain (Kamper et al., 2015).

Due to such a multicomponential nature of pain experience and its widespread neural representation, pain is also strictly linked to, and affected by, other sensory modalities, contributing to the multisensory construction of body representation. In the clinical domain, different studies have assessed the reduction of chronic pain in a limb (or phantom limb in the case of amputation), by looking at a mirror reflecting the image of the intact limb, the so-called mirror box setting for

phantom limb sensations and Complex Regional Pain Syndrome (e.g., McCabe et al., 2003; Ramachandran & Altschuler, 2009). Further evidence gathered from neurologically intact individuals have shown similar reductions of pain by vision of a body part (Longo, Betti, Aglioti, & Haggard, 2009). Also, altering the processes by which the brain localises a noxious stimulus, by crossing the hands, for instance, has analgesic effects, thus, disclosing the relationship between somatotopic and spatial pain localization (Gallace, Torta, Moseley, & Iannetti, 2011; Valentini, Koch, & Aglioti, 2015). The relationship between vision of the body 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).

A critical recent finding is that vision-nociception integration requires intact bodily awareness. In a group of patients affected by somatoparaphrenia, consisting in the denial of ownership of contralesional body parts, Romano and colleagues (2014) have shown an absence of anticipatory responses 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. This suggests a critical role of the sense of body ownership so that the basic mechanisms of response to potential harmful stimuli could be put in place. A logically related finding is that a transfer of body ownership to an avatar, through a Full Body Illusion paradigm, reduces perceived pain (Romano, Pfeiffer, Maravita, & Blanke, 2014).

Intriguingly, as in the case of touch (Kennett, Taylor-Clarke, & Haggard, 2001) and movement (Bernardi et al., 2013; Marino, Stucchi, Nava, Haggard, & Maravita, 2010), distortion of visual feedback about the body can modulate pain perception. Again, inspiration for this comes from the clinical literature, where providing a visual feedback showing reduced size of a body part (or phantom limbs for amputees, through a mirror box paradigm) affected by chronic pain, has analgesic effects (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 increases pain threshold (Mancini, Longo, Kammers, & Haggard, 2011) as well as physiological response to pain (Romano & Maravita, 2014). The work by Romano and Maravita (2014) explored the dynamics of the analgesic response induced by visual magnification of the body, showing that reduced skin conductance response and subjective rating of pain on stimulus contact, is preceded by increased arousal response when the threatening stimulus approaches the body. In other words, pain anticipation is followed by smaller pain response, following visual body magnification. The opposite effects of visual distortion found on chronic and acute pain conditions could be due to the different processing for acute and chronic 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.

In summary, all the above evidence calls for a strict relationship between pain and the other sensory modalities. In particular visual-somatosensory interactions in the peripersonal space are present not only for touch, as known for a long time (Macaluso & Maravita, 2010), but also for pain. This latter modality, unpleasant but highly adaptive, thus provides an important contribution to the multisensory knowledge of our body. It also highlights a tight link between pain perception and the way we represent our bodies, so that even a temporary change in the visual size of the body can modify subjective and neurophysiological responses to pain. These effects are underpinned by mechanisms that still need to be uncovered, that may relay on the modulation of sensory analysis of the body part targeted by an incoming noxious stimulus to the triggering of intracerebral or cortico-spinal analgesic effects at sensory or cognitive-imaginative levels.

### **Visual contribution to body representation**

Unlike the perception of non-corporal objects, the body is always experienced via sensory inputs from several modalities. However, in humans, vision is typically considered the dominant sense as well as the most reliable in terms of spatial perception (Power & Graham, 1976; Rock &

Victor, 1964). Consequently, it seems reasonable to suppose that when visual information is available, perception of one's body dimensions would be relatively accurate. Nevertheless, recent research has found that even neurologically intact individuals have large distortions in the perceptions of their own body proportions, even when looking at their bodies in a mirror (Linkenauger et al., 2015). Specifically, they tend to overestimate the size of each body part, with the magnitude of this effect appearing to vary inversely with respect to the size of the part's representation in the sensory homunculus in the primary somatosensory cortex, which reflects tactile sensitivity, see Figure 1. For instance, the length of less tactilely sensitive body parts, such as the torso, are overestimated more than more sensitive body parts, such as the foot (Linkenauger et al., 2015).

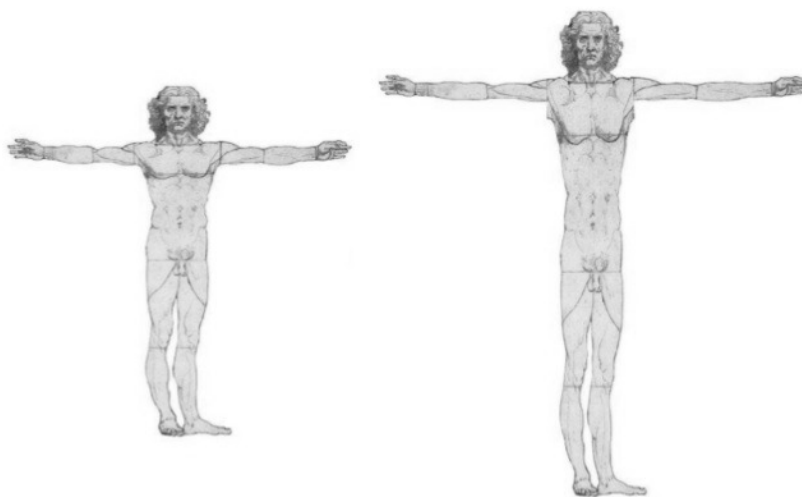


Figure 1. Scaled illustrations of individuals' perceptions of their body proportions (right) and their actual body proportions (left).

Linkenauger and colleagues (2015) interpreted these results in terms of what they called *reverse distortion*, which posits that these distortions originate from a compensatory mechanism in place to achieve adequate tactile size constancy. Specifically, the receptive fields of neurons in 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. This leads to a larger representation in the 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, 1996), which we discuss in more detail below. However, the magnitude of Weber's illusion is only a fraction of the size that it should be if differences in tactile size perception are determined solely by differences in magnification in primary somatosensory cortex (Taylor-Clarke, Jacobsen, & Haggard, 2004).

Consequently, the perceptual system likely has some compensatory mechanism that works to produce a satisfactory degree of tactile size constancy across different body parts. Linkenauger and colleagues (2015) proposed that reverse distortion could serve this role, given that body parts' lengths are distorted in inverse relation to the size of the somatosensory representation, thereby possibly counteracting Weber's illusion. For example, an object may feel smaller on the torso; however, if one experiences their torso as being larger, then the object residing on the torso must also be larger as well. Indeed, it has been found that haptic size perception increases when the RHI is used to make the hand feel larger (Bruno & Bertamini, 2010). Additionally, decreases in a body part's sensitivity via anaesthesia leads to increases in the perception of its size (Gandevia & Phegan, 1999). Chronic pain in a given body part typically reduces the size of the somatosensory representation of that body part and increases the perceived size of the body part (Gandevia & Phegan, 1999; Moseley, 2005). The perceived size of a body part and its somatosensory representation appear to be linked supporting the notion of reverse distortion. However, because so far we have been unable to directly manipulate somatosensory representations or body part size, we cannot be completely sure these distortions are due to reverse distortion rather than some other potential cause. Overall, the evidence from the studies we just described suggests that even with sufficient visual information specifying our body proportions, large distortions are nevertheless present, as we will see in the next section, most likely arising from the influences of the tactile modality.

## **Tactile contributions to body representation**

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 and proprioception 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 (2010) referred to as the ‘body model’. 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 (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 (Ana Tajadura-Jiménez et al., 2012), the RHI (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 (e.g., 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 (e.g., Alloway, Rosenthal, & Burton, 1989) but more circular on glabrous skin (e.g., DiCarlo, Johnson, & Hsiao, 1998). This suggests that the geometry of receptive fields in somatotopic cortical maps may play of fundamental role in shaping the structure of tactile space. Other studies

have revealed similar anisotropies on other skin surfaces, including the forearm (Green, 1982; Le Cornu Knight, Longo, & Bremner, 2014), the face (Longo, Ghosh, & Yahya, in press), and the leg (Green, 1982). This suggests that distortion may be a general feature of the representation of tactile space.

### **Vestibular contributions to body representation**

The vestibular sense, similar to touch, is intimately related to the inner experience of having a body. Like touch, it has a private character that other modalities, such as vision and audition, do not have. Three orthogonal semicircular 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; zu Eulenburg, Baumgärtner, Treede, & Dieterich, 2013; Lopez, Blanke, & Mast, 2012; Lopez & Blanke, 2011), 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, Sedda, Gandola, & Bottini, 2011; Ferrè, Bottini, Iannetti, & Haggard, 2013; Ferrè, Day, Bottini, & Haggard, 2013), 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., 2012b). As we have described in the preceding section, no peripheral receptors are directly informative about such features, and therefore this knowledge is plausibly linked to the body model proposed by Longo and colleagues (2010). Vestibular stimulation increased the perceived length and width of the hand compared to sham stimulation (Lopez, Schreyer, Preuss, & Mast, 2012; but see 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 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 RHI (Botvinick and Cohen, 1998). Combining RHI 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 RHI. However, Lopez et al. (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. While it is difficult to reconcile results from these studies, it is notable that

proprioceptive drift (Ferrè et al., 2015) and questionnaires (Lopez et al., 2010) are two different and independent aspects of the RHI (Rohde, Di Luca, & Ernst, 2011).

Our bodily experiences are tagged by a first-person perspective. This can be seen as a proxy of the spatial unity between the self and the physical body. Recently, Ferrè et al. (2014) investigated whether vestibular signals influence the perspective people take (first-person perspective vs third-person perspective) in interpreting ambiguous tactile stimuli (e.g., graphaesthesia task, 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. 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.

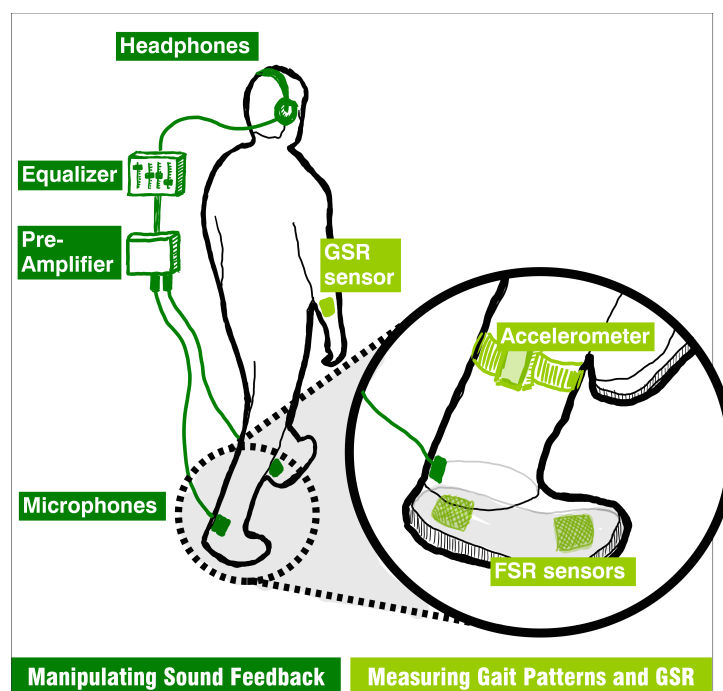
The vestibular system provides fundamental information about the position and motion of the body, relative to the external environment. However, these results suggest that vestibular signals are not only an input for motor control and postural responses, but also a distinct source of information about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

### **Auditory contributions to body representation**

As a final section, we include a neglected modality in the body representation literature. 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, some studies have demonstrated that hearing contributes to body awareness. Apart from these studies, there is some evidence that sounds generated when interacting with objects and surfaces can 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 Jiménez, Larsson, Västfjäll, & Kleiner, 2008). Further, in sports and rehabilitation contexts, sound feedback of body movements is sometimes provided to enhance body and movement awareness (e.g., Cesarini, Hermann, & Ungerechts, 2014; Großhauser, Bläsing, Spieth, & Hermann, 2012; Sigrist, Rauter, Riener, & Wolf, 2013; Singh et al., 2014).



*Figure 2. Manipulating sound-feedback and sensing gait and emotion, adapted from Tajadura-Jiménez et al., 2015. GSR: Galvanic Skin Response; FSR: Force Sensitive Resistor.*

Listening to action related sounds can have an effect on 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; see Pazzaglia, Smania, Corato, & Aglioti, 2008 for related findings in the visual domain). 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).

Finally, a few recent studies have shown that altering action related sounds can elicit changes in the represented body dimensions. 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; Tajadura-Jiménez, Tsakiris, Marquardt, & Bianchi-Berthouze, 2015). Another study showed that 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 (see Figure 2; Tajadura-Jiménez, Basia, et al., 2015). Changes in the walking sounds were also connected to changes in walking behavior and emotional state. In a related study Tonetto and colleagues (2014) showed similar influences of walking sounds in people's emotional state and other bodily sensations.

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 self-esteem.

## **Discussion**

In this review we have attempted to give an overview of the topics discussed in the symposium on Multimodal Contributions to Body Representation (15th International Multisensory Research Forum, Pisa, June 2015). In the light of the talks presented, we have overviewed some of the most recent evidence of the contribution of single sensory modalities to the creation of coherent representations of the body. We have seen how different sensory modalities and their interactions can contribute to form appropriate body representations.

In this respect, we have exposed how a complex neural circuit widespread across different brain areas mediates the sensory experience of pain and has intimate relations with several sensory modalities. We have shown how vision can be very effective in producing an analgesic effect in certain circumstances, such as the ones in which the ownership of the body is preserved. This is a

critical example that emphasise the pivotal role played by the perception of the body in promoting or limiting interactions between the different senses. Despite the fact that vision is the dominant sense as well as the most reliable in terms of spatial perception, recent research has 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 each skin area. This has led researchers to interpret this disparity as a compensatory mechanism necessary to achieve a good degree of tactile size constancy across different body parts.

Perception of the body through touch is thought to be mediated by similar processes of tactile size constancy. For instance, we have seen that the estimated tactile distance on the dorsum of the hand is perceived larger as compared to another body part of identical size (e.g., palm 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. Finally, we have 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 can modify the perceived material we are made of. 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 attention 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 constant information about the body, and “turning off” input from these sensory systems is virtually impossible. The results of the studies reviewed here produce an image of the representation of the body as a multisensory concept. As we showed here, the different senses interact and these interactions are likely to contribute fundamentally to the formation of body representations.

Despite the large amount of evidence reported in this mini-symposium review, useful in delineating the mechanisms by which sensory signals shape the representations of our body, we believe that several key questions nevertheless remain unanswered. Among others, a relevant question is the weight or impact each individual sensory modality has on different body representation. Namely, whether there is a sensory modality that is primarily used to determine the way in which we perceive our body. Vision, as considered the dominant sense in many aspects of cognition and perception, might be expected to be similarly dominant in our 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 special 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. Further, it would be interesting to explore the development of multisensory integration (Burr & Gori,

2012) used to achieve appropriate body representations. 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, when research has focused on the body schema, the body representation traditionally most directly linked to movement, it has been done primarily from the perspective of changes in body posture. Although considered (e.g., 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.

## **Acknowledgements**

EA, LT, and MRL were supported by a grant from the European Research Council (ERC-2013-StG-336050) under the FP7 to MRL. ERF was supported by European Union Seventh Framework Programme (EU FP7) project VERE WP1. AM was supported by a FAR grant from the University of Milano-Bicocca. AT was supported by the ESRC grant ES/K001477/1 (“The hearing body”).

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